Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 40, No. 9, September 1983

Volume 40, n° 9, septembre 1983

Canada

Fisheries and Oceans | Pêches et Océans

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

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Ottawa K1A 0E6

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Dynamics and Environmental Effects of Ice in the Cumberland Basin of the Bay of Fundy

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GORDON, D. C. JR., AND C. DESPLANQUE. 1983. Dynamics and environmental effects of ice in the Cumberland Basin of the Bay of Fundy. Can. J. Fish. Aquat. Sci. 40: 1331–1342.

Ice occurs in the upper reaches of the Bay of Fundy from December to April and conditions are influenced by the macrotides characteristic of the area. Drift ice forms on the seawater surface and because of almost constant movement in tidal currents is composed of small, rounded pieces. Shorefast ice develops from the stranding of drift ice between the neap and spring high water levels. Drift ice can also strand during ebb tide on intertidal salt marshes and mudflats which together comprise two-thirds of the Cumberland Basin area. Intertidal sediments can freeze to form a frozen crust, and sheet ice can form where salinity and tidal energy are low. Shorefast ice can significantly reduce the cross-sectional area of tidal rivers and encourage flooding. Stranded drift ice can import sediment and export plant debris from salt marshes. Mudflats are heavily scoured by ice all winter which causes erosion and mortality of benthic organisms. Construction of a tidal power project would change ice properties considerably.

GORDON, D. C. JR., AND C. DESPLANQUE. 1983. Dynamics and environmental effects of ice in the Cumberland Basin of the Bay of Fundy. Can. J. Fish. Aquat. Sci. 40: 1331–1342.

On trouve de la glace dans les parties supérieures de la baie de Fundy de décembre à avril et les grandes marées caractéristiques de cette région en influencent les conditions. De la glace flottante se forme à la surface des eaux salées et, à cause du mouvement presque constant des courants de marée, elle se compose de petits morceaux ronds. La glace de rive provient de l'échouage de la glace dérivante entre la marée de morte eau et la pleine mer moyenne de vive eau. La glace flottante peut aussi s'échouer pendant la marée descendante dans les veys et les

Printed in Canada (J6910)
Imprimé au Canada (J6910)

marais salants intertidaux qui, ensemble, constituent les deux-tiers de la région du bassin Cumberland. Les sédiments intertidaux peuvent geler pour former une croûte glacée et une nappe de glace peut apparaître là où la salinité et l'énergie marémotrice sont faibles. La glace de rive peut grandement réduire la superficie transversale des rivières à marée et favoriser les inondations. La glace dérivante échouée peut importer des sédiments dans les marais salants et en exporter des débris végétaux. Tout l'hiver, la glace affouille fortement les veys, ce qui entraîne l'érosion et la mort des organismes benthiques. La construction d'une centrale marémotrice changera beaucoup les propriétés de la glace.

Received April 22, 1982
Accepted May 10, 1983

Reçu le 22 avril 1982
Accepté le 10 mai 1983

INTERTIDAL ice is common at higher latitudes and exerts numerous environmental effects, both sedimentological (e.g. Dionne 1969: Knight and Dalrymple 1976; Sasseville and Anderson 1976) and biological (e.g. Ellis and Wilce 1961; Medcof and Thomas 1974; Peterson 1977). Winter ice is widespread in the upper reaches of the Bay of Fundy (Fig. 1) but has received limited scientific attention. With the exception of Knight and Dalrymple (1976) who studied the sedimentological effects of ice on Cobequid Bay, Fundy ice research has focused on potential effects of various proposed engineering projects. For example, Hind (1875) considered the impact of ice on the construction of the Baie Verte Canal (proposed to run from the Cumberland Basin across the Chignecto Isthmus to the Northumberland Strait but never built). More recently, the effects of ice on proposed large-scale tidal power projects have been examined (Atlantic Tidal Power Programming Board 1969). Sweet (1967) reported general ice conditions in Minas Basin, Chignecto Bay, and Annapolis Basin while Desplanque (1967) has studied ice conditions in tidal rivers and estuaries in the same region.

Beginning in 1978 the Marine Ecology Laboratory has been conducting ecological research in the Bay of Fundy region with emphasis upon the Cumberland Basin which is the site that was given highest priority for tidal power development in 1977 (Bay of Fundy Tidal Power Review Board 1977). Field work was conducted year-round and it soon became apparent that ice must play an important role, especially in the extensive intertidal zone of this macrotidal region. Therefore some attention was given to understanding the dynamics and environmental effects of intertidal ice.

This report synthesizes numerous observations and measurements made in the Cumberland Basin and the adjacent part of Chignecto Bay over a number of years but mostly between 1978 and 1981. It draws attention to ice features that appear to be unique in high energy macrotidal environments and illustrates the influence that ice can exert on intertidal ecosystems.

Methods

Many of the observations reported were made by helicopter which allowed us to visit inaccessible locations and to examine ice conditions over a large area in very short time during all stages of the ice season. Observations were also made on a cruise of the C.S.S. *Dawson* which entered Cumberland Basin in February 1980.

A number of sedimentological variables were measured at the Pecks Cove mudflat (Fig. 2). Erosion and deposition over a seasonal cycle were determined at three locations along a transect perpendicular to the shore by measuring with a thin metal probe the depth of sediment above level metal plates (30×30 cm) buried about 20 cm deep. Three plates were placed at each location and six readings were made over each plate. Plate locations were marked by paired wooden stakes placed on either side about 1 m apart (because ice generally removes wooden stakes these were replaced in the late fall with reinforcing rods which protruded only a few centimetres above the sediment surface). Plates were installed on relatively flat areas of the mudflat away from drainage channels. Samples of surface sediment and suspended particulate matter were collected over a seasonal cycle and particle-size distributions were determined using the techniques of Kranck and Milligan (1979).

Environmental Description

Chignecto Bay forms the northern extremity of the Bay of Fundy and branches into Shepody Bay and Cumberland Basin (Fig. 1). The region is famous for its large semidiurnal tides which are among the highest in the world. In Cumberland Basin, the average tidal range is about 11 m (Fig. 3) but varies considerably as a result of the interplay of several tidal generating forces which are easily visible in this macrotidal environment. This variability has a major effect upon the thickness and extent of ice. Over the 14.77-d spring/neap cycle, caused by changes in the position of the sun and moon relative to earth, the elevation of high water commonly varies about 2.5 m. The elevation of high water also follows a 27.55-d cycle caused by the eccentricity of the lunar orbit. During perigee, when the moon is closest to the earth, tides can be about 1 m higher than under apogee conditions. A longer cycle averaging 206 d is caused by interaction of the spring/neap and perigee/apogee cycles with extra strong tides occurring when the times of full (or new) moon and perigee coincide. This cycle, illustrated in Fig. 4, produces up to 10 exceptionally high tides some winters but none during others. There also is the Saros 18.03-yr cycle in the occurrence of extreme tides which last peaked about 1976. Adding all these cycles together, even excluding storm effects, the levels of high and low water can vary as much as 5 m in the upper reaches of the Bay of Fundy any time of year (Fig. 3).

Except for a brief period of slack tide at current reversal (10–20 min), water is constantly moving either in or out of Cumberland Basin at velocities of $0.5-2.0\ \mathrm{m \cdot s^{-1}}$ (Amos and

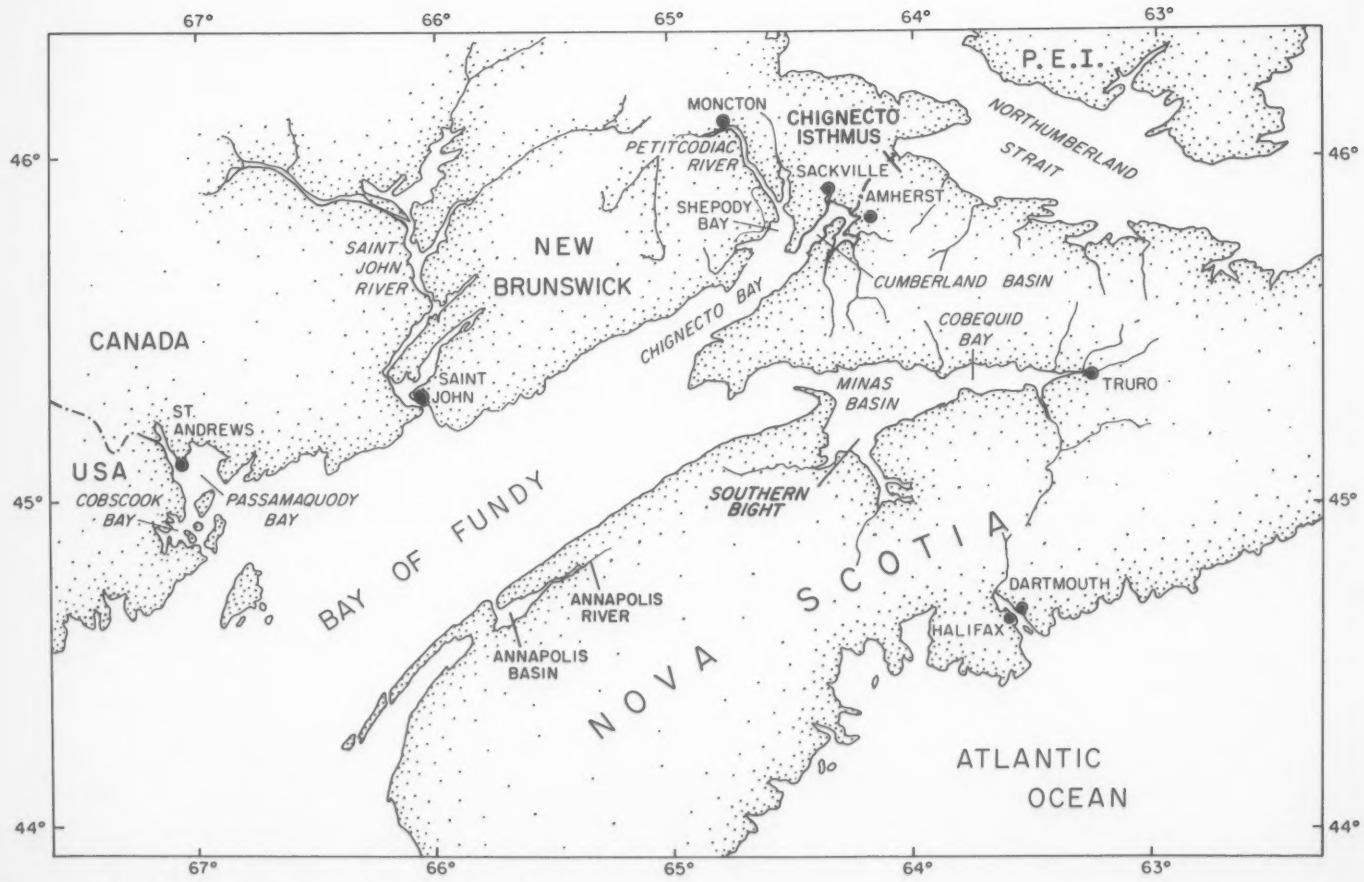

FIG. 1. The Bay of Fundy region showing the location of principal geographic features.

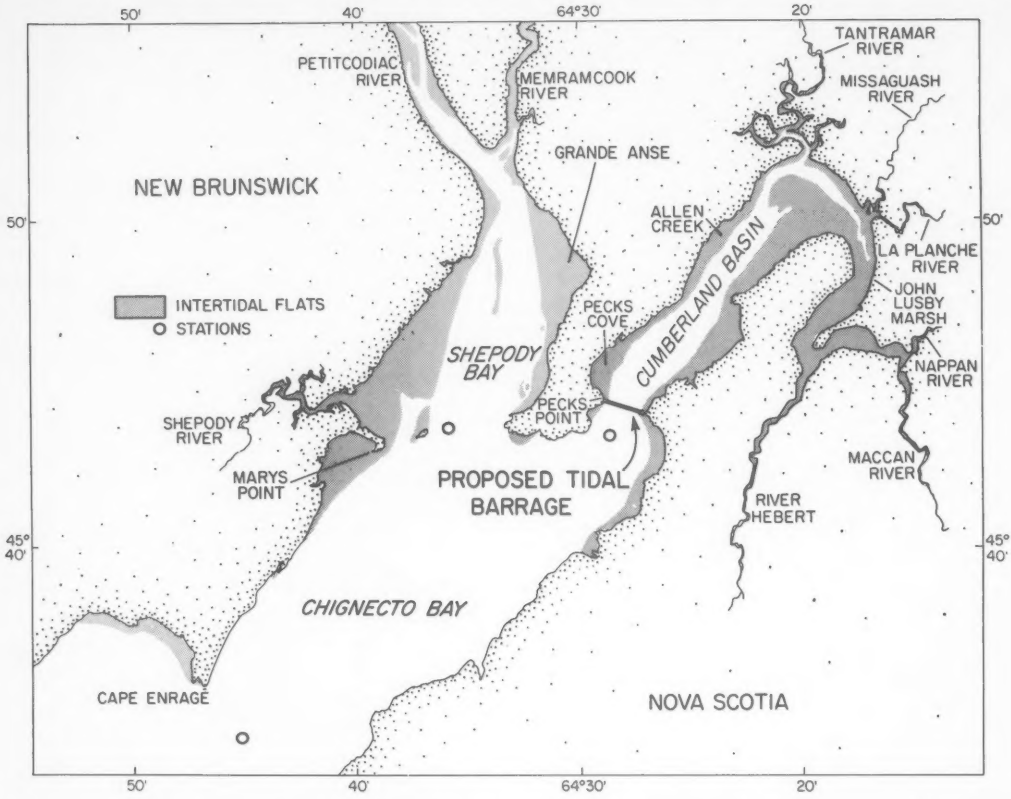

FIG. 2. The upper part of Chignecto Bay showing principal geographic features and extent of intertidal sediments. Circles mark the locations where observations were made on the C.S.S. *Dawson* in February 1980.

Asprey 1981). Although numerous small rivers discharge into the Basin (Fig. 2), the volume of freshwater input is small compared to the twice-daily tidal flushing (Garrett et al. 1978). Salinity is usually greater than 15 ‰ except for the upper parts of the Basin around the time of low water. As a result of excessive tidal energy, the water column is well mixed. Regional climate has been described by Gates and O'Neill 1977.

Two-thirds (79.6 km^2) of the Cumberland Basin is intertidal (Fig. 2). Salt marsh occurs in the high water zone (Fig. 3) and comprises 15% of the total area. About half of the total area is predominantly mudflat having few sediment particles larger than 100 μm (Fig. 5); coarser sediments are commonly found only along narrow beaches or below the mean low water level. Sedimentary rock outcrops are limited and restricted to near the headlands. Suspended sediment concentrations range from $\sim 0.1-0.3$ g L^{-1} at the mouth of Cumberland Basin up to $20-40$ g L^{-1} in tidal rivers near the head (Amos and Asprey 1981; Gordon and Desplanque unpublished data). Particles are generally in the silt range (less than 62 μm) (Fig. 5).

Ice Types and Formation Processes

Knight and Dalrymple (1976) have described the occurrence and formation of ice in Cobequid Bay (Fig. 1). They recognized three principal ice types that are also the most common in Cumberland Basin: drift ice, shorefast ice (or icefoot), and frozen crust.

Drift ice, which is found in various stages of formation (including slush, pans, cakes, and composite ice), forms on the seawater surface. Because of almost constant movement in tidal currents, pieces are generally small (on the order of a few metres or less in diameter) and rounded from frequent collisions (at a mean current speed of 1 $m \cdot s^{-1}$ drift ice can move as far as 20 km in 6 h). Distribution is strongly influenced by the wind, and under the right weather conditions individual pieces of drift ice can temporarily freeze together into a single mass. It commonly strands in the extensive intertidal zone during ebb tide and under the right conditions can freeze to the substrate. Drift ice can contain a considerable amount of sediment of various particles sizes picked up from seawater and substrate (Knight and Dalrymple 1976).

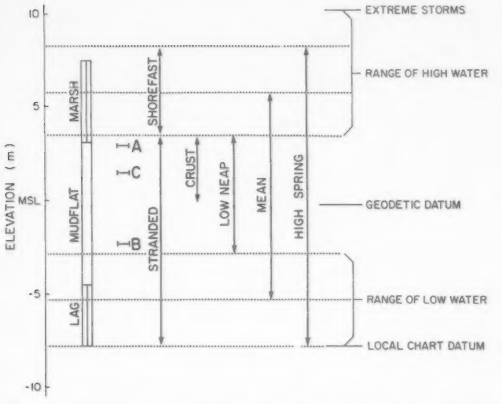

FIG. 3. Range and variation of tidal amplitude in the Cumberland Basin (Canadian Hydrographic Service Tide Tables) and elevations of major features discussed in the paper. Geodetic datum is about 0.2 m below mean sea level (MSL).

Shorefast ice forms along the shoreline in the zone between neap and spring high water (Fig. 6). Although wave action and precipitation are important, the bulk of shorefast ice is formed by the stranding of drift ice at high water when the tide is going from neap to spring conditions or during onshore storms. Repeated freezing and thawing fuses the individual pieces together to form a single mass which is usually frozen to the substrate throughout the winter. The height and width of shorefast ice are dependent upon the slope of the foreshore. The thickest accumulations (5 m and greater) develop where slopes are steep such as along tidal rivers (Fig. 6) and outcrops. The horizontal extent is greatest (up to at least 100 m at times) where slopes are slight bordering the major mudflats, and often the outer portion is not frozen to the bottom but rises and falls with the tide, allowing water movement between the ice and the sediment (Fig. 6). The stranding of drift ice is assisted by the fact that because of inertia, the flooding current does not reverse until about half an hour after high water (Desplanque 1967; Amos and Asprey 1981). Shorefast ice also contains appreciable sediment obtained by several mechanisms which concentrates on the upper surface by progressive melting as winter progresses.

The third major type of ice, frozen crust, forms on the surface of intertidal sediment by both the downward freezing of pore water and the upward accretion of precipitation, runoff, and seawater. It is more extensive at higher elevations where exposure time is longer, and the thickness can range up to 50 cm (Knight and Dalrymple 1976). Where common, frozen crust can protect and immobilize intertidal sediment.

A fourth type of ice not mentioned by Knight and Dalrymple (1976) but important in the upper parts of Cumberland Basin is sheet ice. It is most commonly found in tidal rivers and salt marsh ponds where salinity and tidal energy are much reduced. It generally forms a continuous layer except for fractures caused by tidal fluctuations. Sediment content is very low.

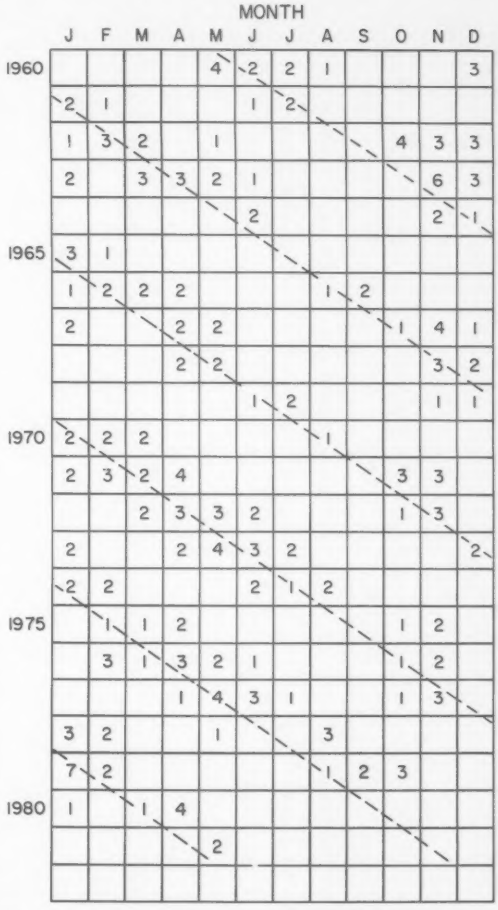

FIG. 4. Frequency of extreme tides in the Bay of Fundy since 1960. Numbers indicate the monthly occurrence of tides exceeding 8.6 m (above chart datum) at Saint John (data for 1981 and 1982 are based on predicted tides). These tides attain an elevation of about 15 m above chart datum in Cumberland Basin and are potentially capable of flooding the extensive flat high marsh areas (Fig. 6). Diagonal lines help illustrate the 206-d cycle in extreme tides.

General Sequence of Ice Events

DECEMBER

Ice formation usually begins in mid-December. Freshwater sheet ice is the first to form. Not long after, drift ice begins to form in the upper part of Cumberland Basin where shallower depths promote more rapid cooling of the water column and salinity is reduced by river discharge (the freezing point varies from 0 to about −1.5°C depending upon salinity). Snow falling on the water will increase the cooling rate. As

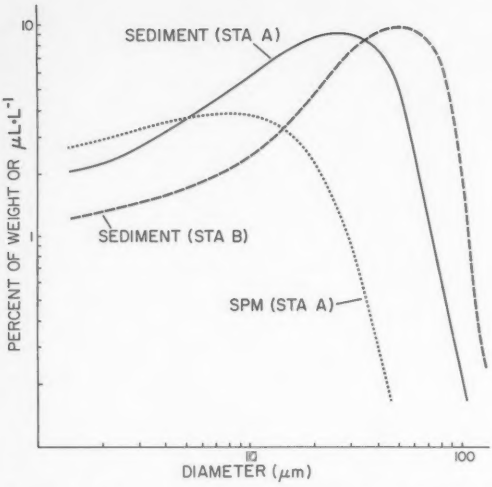

FIG. 5. Particle-size distribution of intertidal surface sediment and suspended particulate matter (SPM) at the Pecks Cove mudflat (Fig. 2). Elevations of stations are shown in Fig. 3. Sediment data expressed as percent weight, SPM as $\mu L \cdot L^{-1}$. Average of numerous samples collected between April and December 1979.

the month progresses, average air and water temperatures drop further and the freezing zone moves seaward to include most of the Basin. Shorefast ice and frozen crust form simultaneously with drift ice, again first and most rapidly in the upper parts of the Basin. By the end of December shorefast ice is generally well developed along the tidal rivers and at headlands, and drift ice extends at least as far as the mouth of the Basin at low tide. Scattered frozen crust can occur as well.

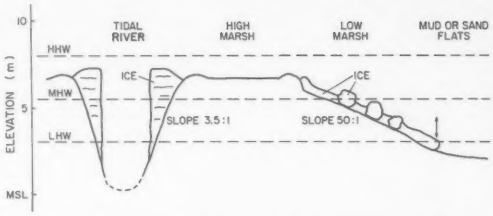

FIG. 6. Different types of shorefast ice along tidal rivers and upper edge of sediment flats. Only during winters of extreme tides can sea ice invade high marsh areas. Lower edge of shorefast ice bordering sediment flats can be floated at high tide.

JANUARY

General ice development continues as the coldest period of the year approaches. Shorefast ice has developed everywhere by the end of the month, even along the beaches landward of the extensive intertidal mudflats (Fig. 7). Along the tidal rivers it has developed into thick vertical ice walls (Fig. 6 and 8). Smaller rivers such as the Tantramar, Missaguash, LaPlanche, and Nappan can form a continuous layer of fractured sheet ice all the way out to their mouths. Stranded drift

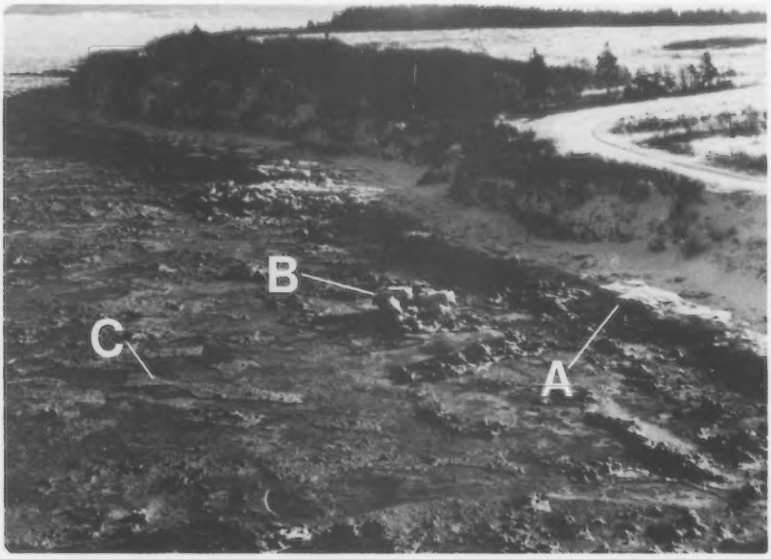

FIG. 7. Pecks Point and the inner portion of the Pecks Cove mudflat showing shorefast ice (A), stranded drift ice (B), and scattered frozen crust (C) (January 12, 1981).

FIG. 8. Shorefast ice along River Hebert which has developed into vertical ice walls 3–4 m high (March 10, 1980). See also Fig. 6.

FIG. 9. Outer portion of the Pecks Cove mudflat taken at an altitude of about 10 m showing scour marks and stranded drift ice (January 26, 1981). Pecks Point in the background.

ice is generally widespread at low tide (Fig. 7) but extremely variable in abundance and distribution. Coverage ranges from 0 to 100% but on average is about 50%, making it relatively easy to observe and sample intertidal sediment. Frozen crust occurs (Fig. 7) but is not widespread, and mudflats are heavily scoured by moving drift ice as the tide rises and falls every

FIG. 10. Continuous drift ice coverage near low tide in Cumberland Basin looking northeast toward Amherst (January 12, 1981). Pecks Point is the second headland on the left.

6 h (Fig. 9). Drift ice usually covers 80–100% of the water and is thickest at high tide, especially in the upper part of the Basin where it chokes the estuaries of tidal rivers. As the tide recedes the drift ice spreads over a larger area (Fig. 10) which can extend as far seaward as Cape Enrage. Freezing conditions are found outside the Cumberland Basin.

FEBRUARY

February is commonly the month with the most extensive ice. Vertical ice walls in the tidal rivers reach their maximum extent, especially during those winters with extreme spring tides (Fig. 4). Stranded drift ice remains widespread and variable. Extensive scouring of intertidal sediment continues except for those regions protected by shorefast ice or frozen crust. The freezing zone and drift ice can extend at least as far as Cape Enrage at low tide, the outer fringe being composed of newly formed slush and pan ice. During the February 1980 cruise, drift ice coverage was almost 100% at the mouth of Cumberland Basin over a complete tidal cycle but was thickest around low tide. Horizontal pressure can produce ridging and rafting, and pieces of drift ice with very high sediment loads can be observed (presumably derived from shorefast ice in tidal rivers). During the entire winter, ice coverage is much greater in Cumberland Basin than it is in neighboring Shepody Bay (Fig. 2).

MARCH

Freezing seawater temperatures and heavy ice coverage extend into March most years. In early March 1968 drift ice occurred as far seaward as Cape Chignecto at the mouth of Chignecto Bay (Fig. 1). March, however, is the major thaw month and ice usually starts to disappear by midmonth. In the tidal rivers ice walls begin to break apart and can take on the appearance of "boulder fields" as a result of rounded shapes and high sediment concentrations on the ice surface. Disintegrating shorefast ice can move about the Basin and pieces up to 5 m high occasionally strand on the mudflats. Frozen crust is largely absent and all mudflats are heavily scoured. Most of the ice is usually gone by the end of the month except for the remains of shorefast ice along tidal rivers which can persist until late April.

Environmental Effects

TIDAL RIVERS

Ice walls significantly reduce the cross-sectional area in tidal rivers (Fig. 6 and 8) and retard the passage of ice and water. Ice dams can form under the right conditions and cause serious flooding upstream.

SALT MARSHES

Low salt marsh (45% of the total marsh area) is composed exclusively of *Spartina alterniflora*. Because of its lower elevation (Fig. 6) it is subjected to ice every winter. Inner portions are usually covered with shorefast ice. At some times and places the entire low marsh zone can be covered but more commonly the outer portions are exposed and drift ice frequently strands, releasing considerable amounts of sediment when the ice melts (Fig. 11). In the spring sediment deposits up to 5 cm thick and several metres in diameter are wide-

FIG. 11. Sediment-laden stranded drift ice melting on low salt marsh near Allen Creek (March 25, 1981). Note how most of the previous year's growth of vegetation has disappeared.

spread on the low marsh surface, indicating that transport by ice is an important mechanism for supplying sediment to Fundy marshes which must continually accrete at a rate of at least 3 $mm \cdot yr^{-1}$ to keep pace with rising mean sea level and increasing tidal amplitude (Amos 1978). When ice disappears in the spring most of the previous year's vegetation is gone and all that remains are a few hardy stalks and the underground rhizomes. Although much of the low marsh vegetation appears to be removed in the fall by tidal action, ice probably promotes the mechanical breakdown and export of overwintering plant material during breakup in the spring.

High marsh (55% of the total marsh area) is composed of several plant species, the most dominant being *Spartina patens*, and is subjected to varying ice conditions due to cycles in the occurrence of extreme tides. During some winters little or no flooding occurs (for example 1977, 1981 and 1982) while in others flooding is frequent (for example 1970, 1971 and 1979). During winters with low spring tides sea ice can penetrate only as far as the channels which drain the high marsh areas. Only freshwater sheet ice and snow (fresh or re-crystallized) covers the high marsh surface, and in the spring vegetation looks no different in quality and quantity than it did the previous fall. Under these conditions ice-mediated import of sediment or export of plant detritus on the high marsh can not take place. However, drift ice can be carried up on to high marsh during those winters with extreme tides. When it occurs, flooding is brief and shallow. Stranded ice will melt in place unless subsequent high tides are capable of floating it off. As described for low marsh areas, melting stranded drift ice can supply sediment to the high marsh. Ice may also play a significant role in the export of marsh vegetation as suggested by Morantz (1976) who conducted observations at the John Lusby Marsh (Fig. 2) during the winter of 1975 when several extreme tides occurred (Fig. 4).

MUDFLATS

The most pronounced environmental effects of ice occur on the extensive intertidal mudflats that are subjected to ice scouring all winter long (Fig. 9). The scour marks are relatively shallow (about 2−3 cm on average) and disappear in about a month after the ice is gone. In contrast to Cobequid Bay (Knight and Dalrymple 1976) frozen crust, although locally important, does not appear to play a major role in immobilizing intertidal sediment in Cumberland Basin. For example, frozen crust was encountered only 20% of the time between January and March in 1979 and 1980 when sediment cores were collected by helicopter at eight different sites widely distributed about the Basin.

The buried plate measurements (Fig. 12) indicate erosion of 7 cm of sediment during the winter of 1979−80 on the outer portion of the Pecks Cove mudflat (Sta B). This erosion is compensated by deposition during the spring and summer. There is also evidence of winter erosion at Sta A near the upper portion of the Pecks Cove mudflat but it was much less, presumably because of the nearness to protective shorefast ice (Fig. 3) and the periodic occurrence of frozen crust. A similar seasonal cycle of erosion and deposition was observed at an ice-affected mudflat in Maine (Anderson et al. 1981).

Concurrent with winter-time mudflat erosion is a pronounced increase in the concentration of suspended sediment throughout the water column of the Chignecto Bay region (Fig. 13). Our observations suggest this increase is caused primarily by the resuspension of ice-scoured sediment.

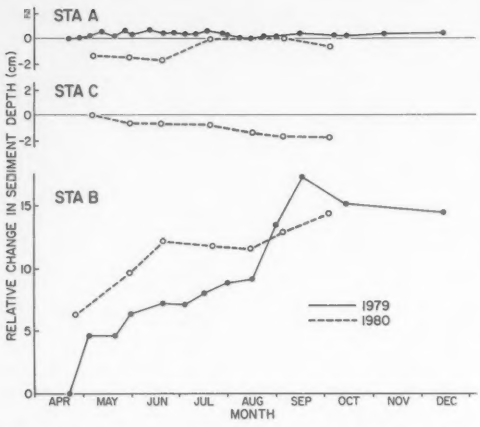

FIG. 12. Erosion/deposition at three sites on the Pecks Cove mudflat as determined using buried plates. All measurements are relative to the initial reading at each site. Station elevations are shown in Fig. 3.

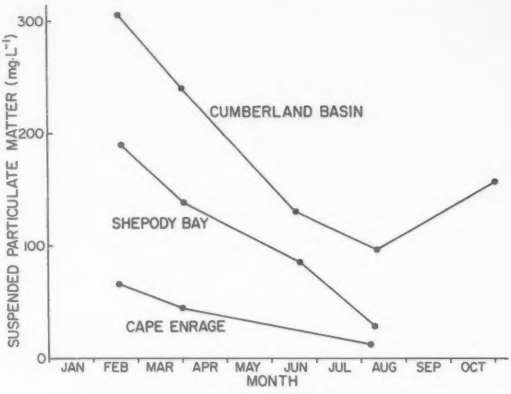

FIG. 13. Average concentrations of suspended particulate matter at three stations in the Chignecto Bay region (Fig. 2). Each value is based on ~50 samples collected at three depths on hourly intervals over a complete tidal cycle. Data from Amos and Asprey (1981) and were collected on five cruises between 1978 and 1980. Data from stations occupied several days apart were averaged together.

However, sediment release from refloated, sediment-laden, stranded drift ice may also constitute a significant source.

Ice imposes a considerable stress on the mudflat ecosystem. Benthic microalgal production in the upper reaches of Fundy is controlled primarily by light availability (Hargrave et al. 1983), and shading by stranded ice may contribute to the very low estimates of winter production. Effects on meiofauna are unknown but probably minor whereas the effects of ice on the macrofauna are major. Macrofaunal diversity is very low and most of the biomass (and production) is composed of just three species: the amphipod *Corophium volutator*, the bivalve *Macoma baltica*, and the polychaete *Heteromastus filiformis* (Hicklin et al. 1980).

Corophium, which is widely distributed across the mudflats, follows a pronounced seasonal cycle of growth during the warmer months and heavy mortality in the winter at all three sites studied by Hicklin et al. (1980). Winter populations are about an order of magnitude less than in summer (Fig. 14). This high winter mortality, also observed by Yeo (1978) in the Minas Basin, does not appear to be caused by biological factors such as food supply or predation because populations in regions not affected by heavy ice show little or no mortality and even some growth during the winter (Watkin 1941; McLusky 1968). *Corophium* is particularly susceptible to ice effects because of its widespread distribution in the surface 3 cm of sediment where scouring is concentrated (Fig. 9). This layer can also be removed over the winter by erosion (Fig. 12) and be frozen solid at times (Fig.7).

The data of Hicklin et al. (1980) do not show significant mortality of *Macoma* or *Heteromastus* during the ice season. The low winter mortality of *Macoma* can be explained by its distribution which may be influenced by ice. Numbers are very low in the middle and outer portions of the mudflats where scouring is most intense (Fig. 3). Most are confined to the inner 200 m of mudflat which receives some protection from frozen crust. At Pecks Cove they are most abundant near

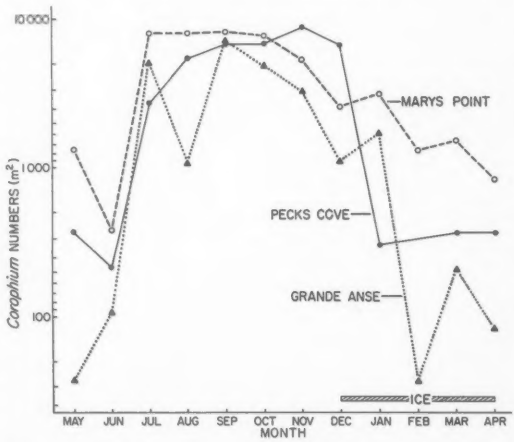

FIG. 14. Seasonal cycle in abundance of *Corophium volutator* at three mudflats in Cumberland Basin and Shepody Bay (Fig. 2). Data from Hicklin et al. (1980) and were collected in 1978 and 1979.

the *Spartina alterniflora* zone (Gordon et al. 1980) which receives considerable protection from shorefast ice. Ice does not appear to have any influence on *Heteromastus* which like *Corophium* is widely distributed over the mudflats, presumably because it can burrow deeper (~10–15 cm) than the zone of scour and erosion.

Discussion

The importance of tidal amplitude in affecting intertidal ice conditions, first recognized by Ellis (1955) on Baffin Island,

is well demonstrated in the Bay of Fundy where the unusually high tides produce a number of conditions not commonly found in other regions.

Although shorefast ice (or ice foot) commonly occurs at other locatons (e.g. Dionne 1969; Ellis and Wilce 1961; Peterson 1977) the phenomenon of thick ice walls (Fig. 8) along tidal rivers appears to be unique to the Bay of Fundy because of the combination of pronounced variation in the elevation of high water over the spring/neap cycle (about 2.5 m) and the abundance of small individual pieces of drift ice that easily strand at high water.

Another unique feature is the significant variability in the elevation of extreme tides over periods longer than the spring/neap cycle (Fig. 4) which affects not only the degree of development of shorefast ice but also the extent to which high marsh (about 8% of the Cumberland Basin area) is influenced by sea ice. In recent years about one third of the winters (defined as January through March) have not had tides high enough to potentially flood high marshes (Fig. 4). No flooding was observed during the winter of 1981 when frequent visits were made. If flooding did occur during these winters, it was shallow and infrequent so ice-mediated import and export processes were probably not important. However, during those winters with extreme tides sea ice has the potential of reaching high marsh areas and influencing the import of sediment and the export of plant debris. Both of these processes have been documented on high marsh areas in the Southern Bight area of the Minas Basin by Bleakney (1972).

In most cold environments, shorefast or stationary sea ice covers the intertidal region for most of the ice season and sediment scouring occurs primarily at breakup (e.g. Dionne 1969; Ellis and Wilce 1961). Our observations in Cumberland Basin indicate, however, that intertidal sediments are subjected to almost continuous ice scour (Fig. 9) all winter long which suggests that frozen crust plays a more limited role in immobilizing sediment than it appears to do in Cobequid Bay (Knight and Dalrymple 1976). The differences in our observations may be related to sediment type, for intertidal sediment in Cumberland Basin is predominantly silt (Fig. 5) whereas sands dominate Cobequid Bay (Yeo and Risk 1981). Bleakney (1972) reports extensive scouring in the Southern Bight area of the Minas Basin which, like Cumberland Basin, has generally finer sediment. Knight and Dalrymple's observations were made only during February, the coldest part of winter, and frozen crust may be less extensive other months. Observations made by helicopter on February 2, 1983, during a very mild winter, indicated little difference in the extent and distribution of frozen crust in Cumberland Basin and Cobequid Bay; it was found only near the high water level in both regions.

Because of variations in weather from year to year the duration of the ice season and its severity can change markedly so that there is probably no such thing as an average year. The beginning and end of the ice season can both vary on the order of a month which can influence the magnitude of environmental effects. This variability must be kept in mind while interpreting data collected during the ice-free season.

Several different mechanisms may be responsible for the high winter mortalities of *Corophium*; direct freezing, disturbance by ice scouring, or loss of substrate due to erosion. As the average low lethal temperature of overwintering *Corophium* is −8.4° (Mills and Fish 1980), mortality by direct freezing is probably minor. In addition, when frozen crust forms, *Corophium* has been seen to migrate laterally and congregate in unfrozen depressions (D. L. Peer, Marine Ecology Laboratory, personal communication). Such movement may explain why *Corophium* distribution is so highly clumped in the early spring. We suggest, therefore, that the winter mortality of *Corophium* is caused primarily by sediment instability. Similar mortalities can also occur outside the ice season because of storms (Yeo and Risk 1979).

As most high-latitude intertidal mollusks are resistant to freezing (Kanwisher 1955; Peterson 1977), it is not surprising that *Macoma* can survive the winter under the protective influence of shorefast ice.

Ice cover was consistently heavier in Cumberland Basin than in nearby Shepody Bay (Fig. 2) during all our observations, and the same pattern was also observed by Sweet (1967). We believe this phenomenon is caused by the prevailing westerly winds (Gates and O'Neill 1977) which push ice eastward, combined with the residual circulation of Chignecto Bay which is inward along the Nova Scotian coast (Amos and Asprey 1981). Some of the eddies predicted by Greenberg (1983) could also help concentrate drift ice near the mouth of the Cumberland Basin.

Construction of a tidal power project in the upper reaches of the Bay of Fundy would markedly change ice conditions. Reducing tidal energy will probably result in water column stratification (Garrett et al. 1978) which could lengthen the ice season. If the velocities of tidal currents in the headpond are reduced significantly, coupled with the freshening of surface water by stratification, the coverage of sheet ice could expand near the tidal rivers. For example, construction of a causeway across the mouth of the Annapolis Estuary (Fig. 1) removed most of the tidal energy and now a continuous layer of sheet ice forms each winter (Sweet 1967) (this situation may change after 1983 when the pilot tidal power project goes into operation and increases tidal influence). By excluding extreme tides, a project would retard the development of shorefast ice, including the ice walls along tidal rivers, and prevent sea ice from reaching the high marsh areas. Substantial reduction of the intertidal zone (by about half) will lessen the area subjected to ice scour and erosion. Accumulation of drift ice at the barrage may also cause some engineering problems that should be considered in project design.

Acknowledgments

We thank the Canadian Coast Guard for the helicopter time that made many of our observations possible and our numerous colleagues for sharing their observations with us. Many co-workers helped with the buried plate measurements. Grain size analyses were kindly conducted by K. Kranck, and E. MacDormand compiled much of the sediment data. The observed tidal elevation data at Saint John were provided by MEDS. We thank P. Keizer, D. Peer, D. Greenberg, and F. Anderson for their comments on earlier drafts of this manuscript.

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Hypolimnetic Aeration of A Naturally Eutrophic Lake: Physical and Chemical Effects

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ASHLEY, K. I. 1983. Hypolimnetic aeration of a naturally eutrophic lake: physical and chemical effects. Can. J. Fish. Aquat. Sci. 40: 1343 – 1359.

To examine the effect of hypolimnetic aeration on key components (circulation, decomposition, major nutrients, major ions, and pH interactions) of a lake ecosystem, I used a small naturally eutrophic lake. I divided the lake in half with a plastic curtain, and installed and operated a hypolimnetic aerator in the experimental half for a year. Hypolimnetic aeration had no effect on thermal stratification during the ice-free season but circulated the entire experimental half under ice cover. Aeration increased hypolimnetic turbidity via reduced detrital sedimentation but did not affect epilimnetic transparency. Hypolimnetic oxygen concentrations were increased as was oxygen consumption as both sediment and water column oxidation of organic material was enhanced. Hypolimnetic ammonia concentrations were reduced and sufficient oxygen was added for nitrification to occur. Internal phosphorous loading and hypolimnetic orthophosphate concentrations were reduced but aerobic P regeneration increased. Aeration vented accumulated CO_2 from the hypolimnion and decreased its calcium, magnesium, bicarbonate, and orthophosphate content via calcium carbonate phosphate coprecipitation. Management applications of hypolimnetic aeration include reduction of internal nutrient loading for eutrophication control, improvement of water quality for domestic use, and prevention of fish winterkill.

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Pour étudier l'incidence de l'aération hypolimnique sur des composantes clés (circulation, décomposition, bioéléments principaux, principales interactions entre les ions et le pH) d'un système lacustre, nous avons divisé à l'aide d'un rideau de plastique un petit lac eutrophe à l'état naturel et nous avons installé et fait fonctionner pendant un an un aérateur hypolimnique dans la moitié expérimentale. L'aération hypolimnique n'a eu aucune incidence sur la stratification thermique pendant la saison libre de glace, mais a réussi à faire circuler toute la partie expérimentale sous la couverture de glace. L'aération a fait augmenter la turbidité de l'hypolimnion par voie d'une sédimentation réduite des détritus mais n'a eu aucune incidence sur la transparence de l'épilimnion. Les concentrations d'oxygène dans l'hypolimnion ont augmenté, tout comme la consommation d'oxygène à cause d'un accroissement de l'oxydation des matières organiques présentes dans les sédiments et la colonne d'eau. Les concentrations d'ammoniac ont diminué et il y a eu un apport suffisant d'oxygène pour permettre la nitrification. La charge interne de phosphore et les concentrations d'orthophosphate dans l'hypolimnion ont été réduites mais la régénération aérobique du P a augmenté. L'aération a fait remonter le CO_2 accumulé dans l'hypolimnion et a réduit son contenu en calcium, en magnésium, en bicarbonate et en orthophosphate par la coprécipitation calcium–carbonate–phosphate. Les applications gestionnelles de l'aération hypolimnique comprennent la réduction de la charge interne de bioéléments pour empêcher l'eutrophisation, l'amélioration de la qualité de l'eau pour l'utiliser à des fins domestiques et la prévention de la mortalité hivernale excessive des poissons.

Received October 13, 1982
Accepted May 12, 1983

Reçu le 13 octobre 1982
Accepté le 12 mai 1983

SINCE its inception in 1949 (Mercier and Perret 1949) more than 20 papers have appeared in the scientific literature describing various hypolimnetic aeration studies (see Taggart and McQueen 1981 for review). Most early aeration projects were descriptive; the best documented projects, however, (Garrell et al. 1977; Smith et al. 1975; Taggart and McQueen 1981) were confounded by external nutrient addition during the experimental period or unintentional destratification (Fast 1971). As a result, conflicting interpretations have appeared in the literature, and the effect of hypolimnetic aeration on various components of the lake ecosystem remains unresolved.

Printed in Canada (J7083)
Imprimé au Canada (J7083)

The purpose of my study was to examine specific components of the lake ecosystem which I believed were poorly understood in terms of their response to hypolimnetic aeration:

1) Circulation processes. Hypolimnetic aeration accelerates circulation currents within the hypolimnion and may increase the vertical exchange of nutrients across the thermocline. This could have serious consequences if nutrients were delivered to the epilimnion during summer stratification (Fast 1971).

2) Decomposition processes. Theoretical (Fillos 1977) and experimental (Smith et al. 1975) evidence suggests hypolimnetic aeration stimulates a three- to four-fold increase in hypolimnetic oxygen consumption. Hypolimnetic aeration may significantly increase sediment and water column oxygen consumption via increased oxygen levels and reduced detrital sedimentation.

3) Major nutrients. Mortimer's (1941–42) theory of P release is well documented in the literature; however, recent evidence indicates P release is influenced by lake type, sediment composition, and historical nutrient loading in addition to ambient oxygen concentrations (Lee 1970; Schindler et al. 1977, 1980). Hypolimnetic aeration should reduce P release by oxygenating the hypolimnion; however, different precipitation mechanisms may operate in eutrophic softwater and hardwater lakes.

The influence of hypolimnetic aeration on the nitrogen cycle is largely unknown, although Chen et al. (1979) predict significant N loss based on laboratory experiments. The "split-lake" experimental approach (Schindler 1974) should eliminate design problems and provide insight into the nitrogen cycle during hypolimnetic aeration.

4) Major ions. Three major ions (Ca^{+2}, Mg^{+2}, HCO_3^-) may be involved in hypolimnetic aeration reactions. Preliminary studies have postulated that $CaCO_3$ precipitation occurs during hypolimnetic aeration of hardwater lakes (Fast et al. 1973). I believe this could reduce phosphorus concentrations via calcium carbonate coprecipitation.

Sediment release of redox-sensitive metals (Mn, Fe) under reducing conditions is a well-known phenomenon (Wetzel 1975). Hypolimnetic aeration should oxidize reduced metals and improve water quality for specific aquatic organisms (Ingols 1975). In addition, oxidation and reduction of Mn and Fe compounds may be involved in P precipitation which should occur during hypolimnetic aeration of eutrophic lakes (Fast 1975; Mortimer 1971).

5) pH interactions. Fast (1971) observed increased pH values following hypolimnetic aeration of a small hardwater lake. If aeration increases pH this could influence lake metabolism by increasing ammonia volatilization (Stratton 1969), decreasing hypolimnetic carbon dioxide concentrations (Sawyer and McCarty 1978) and stimulating major ion (HCO_3^-, Ca^{+2}, Mg^{+2}) and phosphorus coprecipitation (Otsuki and Wetzel 1972).

Study Area and Lake Morphometry

Black Lake is located (elevation 750 m, 49°20′30″N, 119°44′05″W) in the Southern Interior Plateau limnological region of British Columbia (Northcote and Larkin 1956). The region experiences a mild continental climate with low annual precipitation (25 cm) and average air temperatures of 22°C in summer and −3.3°C in winter (Climate of British Columbia 1976). Black Lake originated as part of nearby Yellow Lake, whose basin was cut into volcanic rock by a major meltwater outflow which drained the Kaledon tongue of the main Okanagan ice lobe ~8900 yr ago (Nasmith 1962).

Black Lake (Fig. 1) is naturally eutrophic with historically low levels of dissolved oxygen (Halsey and MacDonald 1971). Maximum depth (9 m) is quite deep for its surface area (3.9 ha) and the lake lies in a steep, narrow valley at right angles to prevailing north–south winds. As a result, Black Lake circulates occasionally (once every 1–2 yr) and exhibits temporary "morphometric meromixis" (Northcote and Halsey 1969).

Materials and Methods

Aeration and Lake Curtain

The hypolimnetic aerator I used was based on designs of Bernhardt and Wilhelms (1975), Hess (1975), and Smith et al. (1975). The aerator consisted of an insulated open box (2.4 × 1.2 × 0.9 m) constructed of 19-mm plywood and 5 cm × 10 cm framing (Fig. 2). A pontoon (0.3 × 0.3 × 2.4 m) was attached to each side of the box and provided 360 kg of positive buoyancy. Two 0.76-m-circular holes were cut in the bottom of the box through which 0.76 m × 7.3 m galvanized steel pipes were fitted. An air diffuser was installed 0.3 m inside the bottom of the intake pipe. The outlet pipe was fitted with a 45° elbow to prevent recirculation of aerated water. The entire unit weighed 453 kg and was securely positioned above the 9-m contour. A new 7.5-kW rotary vane compressor (Hydrovane SR 4000, rated 1.13 m^3/min at 7.0 kg/cm^2) was installed in a shed constructed near the shoreline and connected to the aerator by a weighted airline (106 m × 1.9 cm ID).

The lake was divided into approximately equal sections by a transparent woven polyethylene curtain (Fig. 1, Table 1). The main section (103 m × 10.4 m × 0.4 mm) was composed of DuPont Fabrene type P. The curtain was laid in position on the ice surface (20 cm thick) and the entire length (103 m) cut open with chain saws. A floatline was strung through a surface collar and 113 kg of lead rope attached to its lower edge. The curtain was then pushed into place and sunk into position. Rocks piled on nearshore areas ensured a snug fit and SCUBA observation confirmed the lower edge was well sealed into the sediment. The surface collar floated 10 cm above the water surface and minimized surface water exchange.

Sampling: Physical and Chemical

All samples were collected from permanent sampling stations located near the center of the lake ~20 m apart on either side of the curtain (Fig. 1). These sites were defined as experimental and control stations. The experimental station was 10 m from the aerator and situated at right angles to the aerator outlet tube to avoid sampling directly in the plume of aerated water. Samples were taken every 2 wk from April to October 1978, and at 3-wk intervals from November to March 1979.

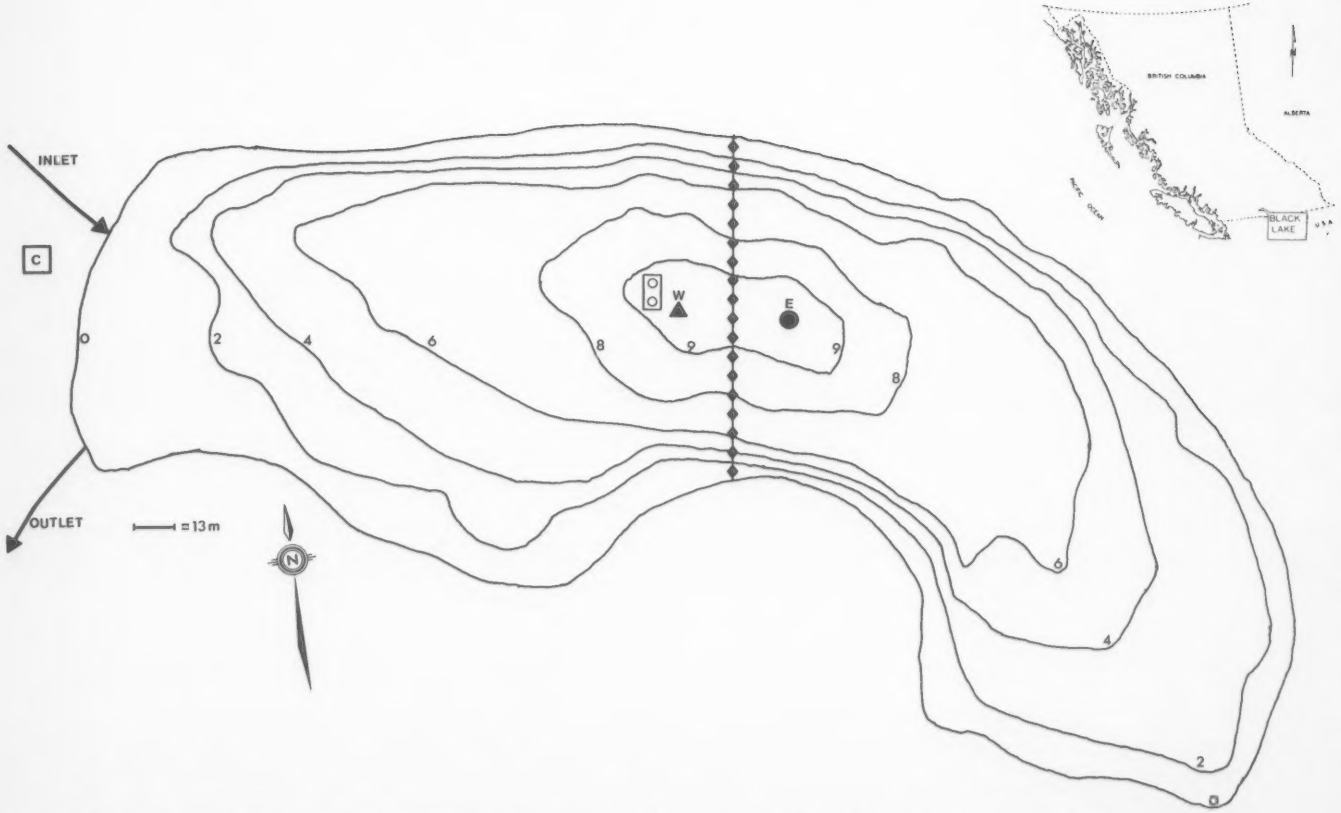

FIG. 1. Black Lake showing depth contours (m), compressor site [C], curtain position ‡, aerator location [ ], and sampling sites (experimental ▲ and control ●).

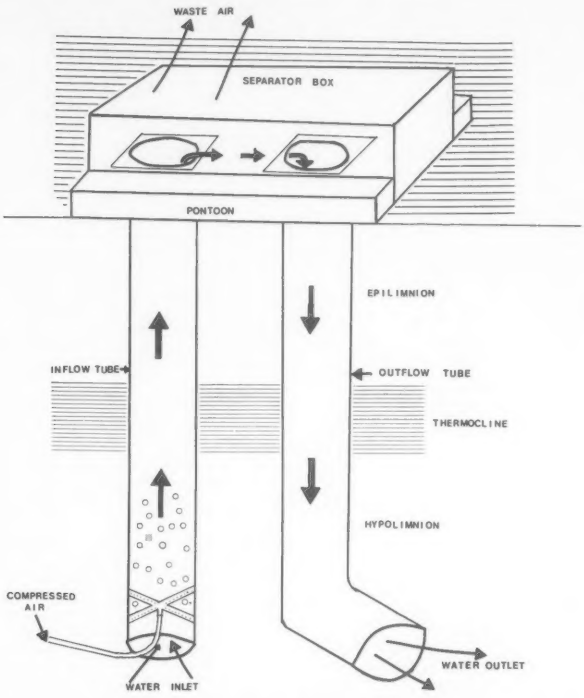

FIG. 2. Schematic diagram of the Black Lake hypolimnetic aerator.

TABLE 1. Area (m^2) and volume (m^3) of Black Lake, experimental side, and control side in 1-m depth intervals.

	Whole lake			Experimental		Control	
Z	Area (m^2)	Strata	Vol. (m^3)	Area	Vol.	Area	Vol.
0	39456	0–1	37464	20204	19047	19252	18417
1	35506	1–2	32850	17912	15965	17594	16885
2	30279	2–3	27652	14094	13261	16185	14391
3	25114	3–4	23206	12445	11407	12669	11799
4	21350	4–5	19662	10400	9512	10950	10150
5	18020	5–6	16041	8650	7791	9370	8250
6	14141	6–7	11967	6962	5988	7179	5979
7	9920	7–8	6975	5065	3602	4855	3373
8	4399	8–9	2726	2316	1398	2083	1328
9	1348			651		697	
		Total	178543		87971		90572

Physical data were collected at 1-m depth intervals. Temperature series were taken with a thermistor (YSI model 54 ARC). Transparency was measured with a standard 20-cm Secchi disk using a glass-bottom viewing box. Percent light transmission was obtained with a simple photocell (Beckman EV3) light meter.

Dissolved oxygen was measured at 1-m intervals with an oxygen meter (YSI model 54 ARC). Replicate ($n = 2$) Winkler titrations (Azide modification) were used to calibrate the meter at surface concentrations during each sampling trip. All other chemical parameters were collected at 2-m intervals with an electric pump (Jabsco, at 26 L/min). Samples were poured into polyethylene bottles, stored at 0°C in sealed containers and transported to the laboratory within 24 h. The Environmental Laboratory (Water Resource Service, Ministry of the Environment, 3650 Wesbrook, UBC) performed all analyses according to their methods manual (Water Resources Service 1976). All samples were analyzed within 48 h of sampling, except for Mn and Fe which were preserved with nitric acid and stored for up to 14 d at room temperature.

Water flow was measured with a recently calibrated flowmeter (General Oceanics No. 2035). Oxygen was measured in the downflow tube at a depth of 4 m with a Winkler calibrated oxygen meter. Oxygen transfer ($kg\ O_2^{-1}/d^{-1}$) was calculated as the difference between oxygen concentrations in the inflow tube (9 m) and the outflow tube (4 m) multiplied by volume flow.

I used a two-way ANOVA program to analyze the Black Lake data at the 1% level of significance. The method is outlined in Gilbert (1972).

Results

Air bubbles rising up the inflow tube acted as an air-lift

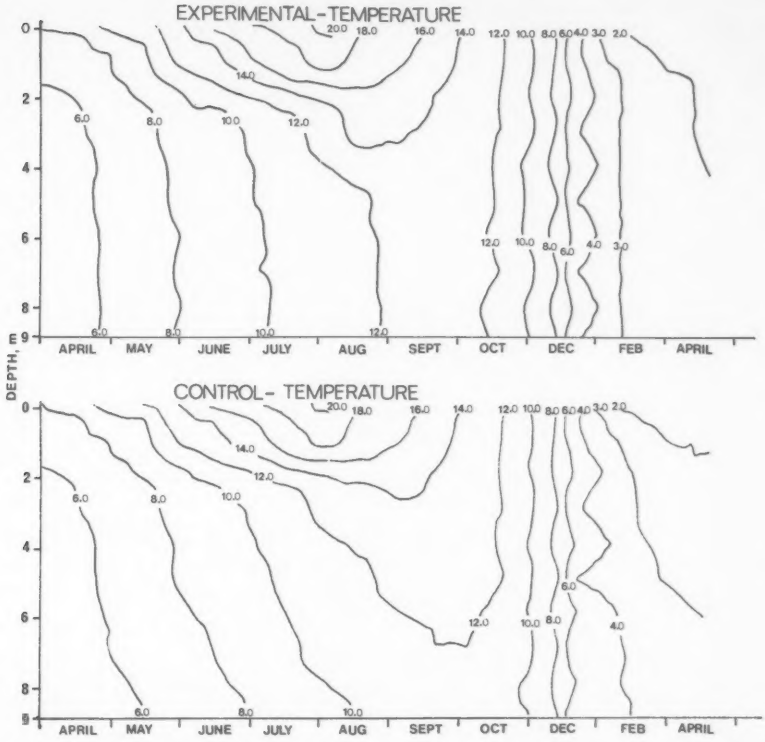

FIG. 3. Temperature isopleths (°C) for experimental and control sides of Black Lake from 1978 to 1979.

pump and generated a large volume−low velocity water flow. The air−water plume rose 10 cm above the water surface in the separator box while degassing, then flowed across the box towards the downflow tube. Aerated water then entered the downflow tube and discharged back into the hypolimnion. Water flow was measured at 10.67 m^3/min which generated a daily flow of 15365 m^3/d. Theoretical hypolimnetic circulation time (hypolimnion volume 18779 m^3) was 1.2 d, and 5.7 d was required to circulate the entire experimental side (87971 m^3) under ice cover.

Thermal stratification was maintained throughout spring, summer, and fall on both sides (Fig. 3). Hypolimnetic aeration under ice cover circulated the entire experimental side (except for microstratification at 0−1 m) as the weak inverse stratification could not resist mixing currents generated by the aerator.

Secchi disk transparency and 1% transmission depths followed similar seasonal trends on both sides (Fig. 4); however, control side values were noticeably (>1 m) greater during summer months.

OXYGEN

The aerator increased oxygen by an average of 0.7 mg/L ($n = 7$) on each cycle through the system. Water flow was constant at 15365 m^3/d, therefore a total of 10.76 kg O_2/d was added to the experimental hypolimnion (5−9 m). Hypolimnetic oxygen concentrations remained below saturation all summer (10 mg/L); however, near-bottom values (9 m) in the experimental side were considerably higher (2.7 mg/L avg.) than in the control side (0.2 mg/L avg.) (Fig. 5). Surface values were similar on both sides and averaged 8.5 mg/L from May until August. The lake froze on November 14 and the maximum recorded oxygen concentration at freeze-up was 8.5 mg/L. Experimental oxygen concentrations remained above 4.9 mg/L all winter whereas control concentrations declined markedly, and less than 1.0 mg/L was present in the lowermost strata (8−9 m) from January 23 to March 6.

Hypolimnetic aeration stimulated oxygen consumption as experimental hypolimnetic oxygen depletion rates were considerably higher (0.39−0.78 $mg \cdot L^{-1} \cdot d^{-1}$) than control values (0.03−0.09 $mg \cdot L^{-1} \cdot d^{-1}$) and ranged from 68 to 137% of daily oxygen loading (10.76 kg/d) (Table 2). Summer and winter oxygen depletion rates were variable; however, winter values (0.39−0.61 $mg \cdot L^{-1} \cdot d^{-1}$ experimental; 0.04−0.06 $mg \cdot L^{-1} \cdot d^{-1}$ control) were generally lower than summer values (0.46−0.78 $mg \cdot L^{-1} \cdot d^{-1}$ experimental; 0.03−0.09 $mg \cdot L^{-1} \cdot d^{-1}$ control). Oxygen

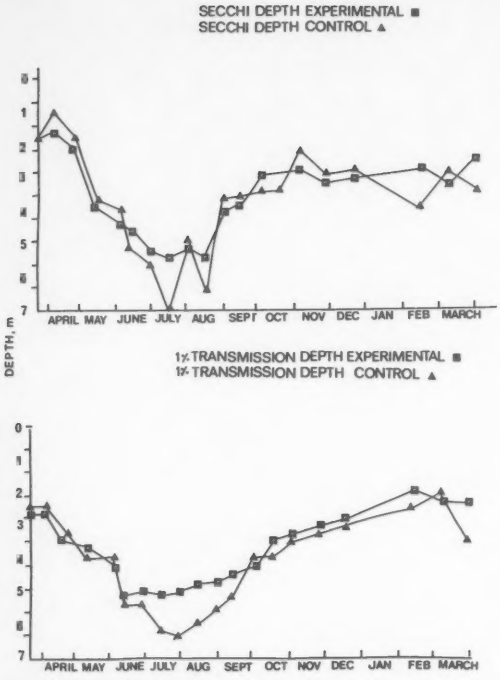
SECCHI DEPTH EXPERIMENTAL ■
SECCHI DEPTH CONTROL ▲
DEPTH, m
APRIL MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MARCH
1% TRANSMISSION DEPTH EXPERIMENTAL ■
1% TRANSMISSION DEPTH CONTROL ▲
APRIL MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MARCH

FIG. 4. Secchi and 1% transmission depths (m) for experimental and control sides of Black Lake from 1978 to 1979.

concentrations were significantly higher (two-way ANOVA, $P < 0.01$) on the experimental side.

NITROGEN

The immediate effect of experimental aeration was a marked reduction in hypolimnetic NH_3-N concentrations. Hypolimnetic (9 m) NH_3-N concentrations gradually increased during summer; however, experimental values (0.300 mg/L avg.) remained considerably lower than control values (1.741 mg/L avg.) (Fig. 6). Surface concentrations of NH_3-N were similar on both sides, averaging 0.033 mg/L (aerated) and 0.036 mg/L (control). NH_3-N concentrations on both sides were evenly distributed beneath ice cover and changed little during winter, except for increasing concentrations in the control hypolimnion. NH_3-N concentrations were significantly (two-way ANOVA, $P < 0.01$) lower on the experimental side.

NO_3-N first appeared in measurable concentrations (>0.02 mg/L) on June 13, and increased during summer from 0.05 (June 13) to 0.12 mg/L (August 29) (Fig. 7). Control side-bottom concentrations remained low and 9-m NO_3-N concentrations were undetectable until October 24. Surface NO_3-N was consistently low all summer, ranging from 0.02 to 0.04 mg/L (experimental) and 0.02 to 0.08 mg/L (control). NO_3-N was homogeneously distributed at 0.33−0.34 mg/L on both sides at ice formation and increased to 0.50 (experimental) and 0.48 mg/L (control) as winter progressed. NO_3-N concentrations were significantly (two-way ANOVA, $P < 0.01$) higher in the experimental hypolimnion. Total nitrogen (epilimnion, 0−5 m) exhibited similar trends on both sides (Fig. 8).

PHOSPHORUS

After 2 wk aeration experimental 8- and 9-m PO_4-P declined from 1100 μg/L to 321−322 μg/L, whereas control 8- and 9-m PO_4-P remained at 735−955 μg/L (Fig. 9). Hypolimnetic (9 m) values on the experimental side averaged 405 μg/L during summer and increased from 344 μg/L (May 9) to 480 μg/L (August 15). Control side 9-m values were much higher (682 μg/L avg.) and increased from 625 μg/L (May 9) to 809 μg/L (August 29). Epilimnetic PO_4-P concentrations averaged 284 μg/L on both sides during summer. PO_4-P stratification was eliminated during fall circulation, became isochemical at 360 μg/L in late October, and remained near 350 μg/L on both sides during winter. PO_4-P concentrations were significantly (two-way ANOVA, $P < 0.01$) lower in the experimental hypolimnion.

Hypolimnetic aeration increased the concentration of dissolved organic phosphate (DOP) and particulate phosphate (PP) in the experimental hypolimnion (Fig. 10). Although both DOP and particulate phosphate were significantly higher (two-way ANOVA, $P < 0.01$), total P (whole lake and epilimnion 0−5 m) remained lower on the experimental side (Fig. 11 and 12).

MAJOR IONS

Experimental hypolimnion (9 m) alkalinity remained much lower all summer, averaging 199 mg/L as compared to 241 mg/L in the control hypolimnion (Fig. 13). Epilimnetic alkalinity was not affected by the experimental treatment as both sides averaged 197 mg/L through summer. Fall circulation eliminated alkalinity stratification and both sides maintained similar concentrations throughout winter.

Experimental hypolimnetic (9 m) calcium declined from 49 to 43 mg/L following 2 wk aeration whereas control values increased from 49 to 51 mg/L. This effect persisted all summer (43 mg/L average experimental; 58 mg/L average control), eventually disappearing at fall circulation (Fig. 14). Epilimnetic calcium was not affected and both sides averaged 42 mg/L during summer. Winter concentrations were similar on both sides. Magnesium ions responded in an analogous fashion i.e. lower hypolimnetic concentrations during summer (13 mg/L avg. experimental; 18 mg/L avg. control), similar epilimnetic concentrations (11.6 mg/L avg.), and equivalent concentrations on both sides through winter.

Experimental dissolved manganese (<0.45 μ) was reduced below detection limits (0.02 mg/L) within 2 wk (Fig. 15) whereas dissolved manganese in the control hypolimnion remained high (0.88−1.04 mg/L). Hypolimnetic (9 m) concentrations on the experimental side remained an order of magnitude lower (0.20 mg/L avg.) than control values (1.15 mg/L avg.) all summer and surface values were similar on both sides (usually <0.02 mg/L). Dissolved manganese

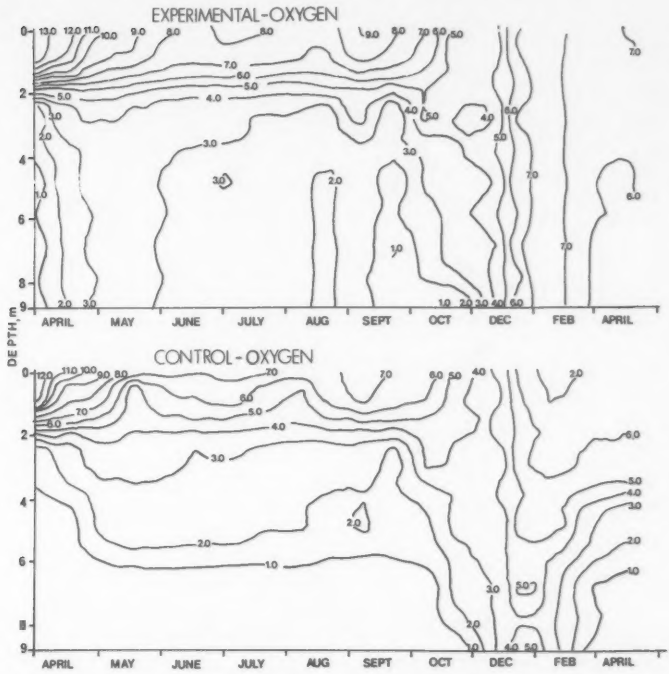

FIG. 5. Oxygen (mg/L) isopleths for experimental and control sides of Black Lake from 1978 to 1979.

TABLE 2. Hypolimnetic (5–9 m) oxygen depletion rates for experimental and control sides of Black Lake.

Experimental side					Control side				
Input[a]	Net loss[b]	mg·L^{-1}·d^{-1}	%/d[c]	Period	Input[a]	Net loss[b]	mg·L^{-1}·d^{-1}	%/d[c]	Period
139.88	98.46	0.40	70.4	April 12–25	—[d]	—[e]	—[e]	—[d]	April 12–25
161.40	139.53	0.49	86.5	April 25–May 9	—	—	—	—	April 25–May 9
161.40	164.30	0.58	101.8	May 9–24	—	—	—	—	May 9–24
204.44	216.39	0.61	105.8	May 24–June 13	—	0.90	0.003	—	May 24–June 13
75.32	78.32	0.60	103.9	June 13–20	—	4.06	0.03	—	June 13–20
161.40	154.65	0.55	95.8	June 20–July 5	—	—	—	—	June 20–July 5
139.88	156.01	0.64	111.5	July 5–18	—	7.12	0.03	—	July 5–18
150.64	143.21	0.55	95.1	July 18–Aug. 1	—	—	—	—	July 18–Aug. 1
150.64	168.38	0.64	111.8	Aug. 1–15	—	12.16	0.05	—	Aug. 1–15
150.64	121.18	0.46	80.4	Aug. 15–29	—	—	—	—	Aug. 15–29
118.36	161.78	0.78	136.7	Aug. 29–Sept. 10	—	19.31	0.09	—	Aug. 29–Sept. 10
182.92	140.45	0.44	76.8	Sept. 10–26	—	—	—	—	Sept. 10–26
150.64	140.39	0.53	93.2	Sept. 26–Oct. 11	—	—	—	—	Sept. 26–Oct. 11
150.64	153.76	0.58	102.1	Oct. 11–24	—	9.07	0.03	—	Oct. 11–24
225.96	154.29	0.39	68.3	Oct. 24–Nov. 14	—	—	—	—	Oct. 24–Nov. 14
225.96	229.76	0.58	101.7	Nov. 14–Dec. 5	—	23.34	0.06	—	Nov. 14–Dec. 5
527.24	548.23	0.60	103.9	Dec. 5–Jan. 24	—	36.49	0.04	—	Dec. 5–Jan. 24
215.20	227.10	0.61	105.5	Jan. 24–Feb. 14	—	13.47	0.04	—	Jan. 24–Feb. 14
225.96	206.77	0.52	91.5	Feb. 14–March 7	—	—	—	—	Feb. 14–March 7

[a]Input of oxygen from aerator (at 10.76 kg O_2/d).
[b]Net loss of hypolimnetic oxygen (kg).
[c]Oxygen consumption as a percentage of daily aerator input.
[d]Not applicable.
[e]Positive values not analyzed.

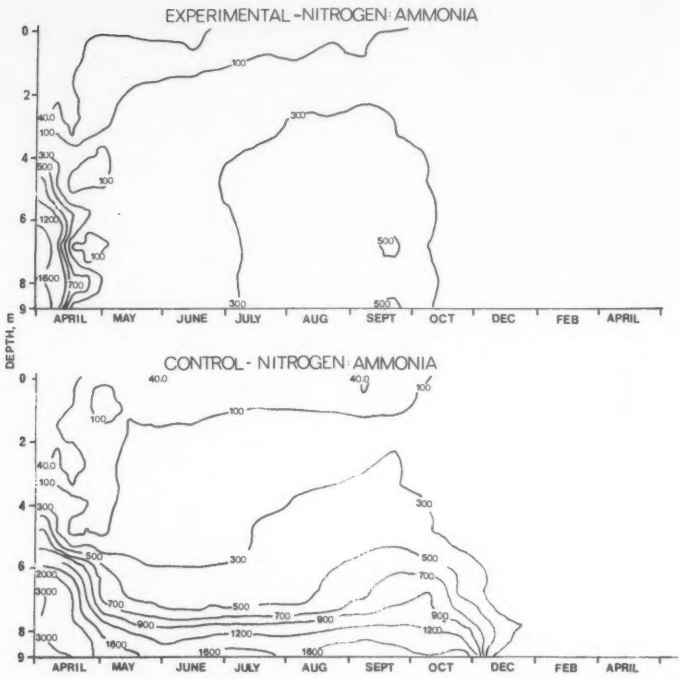

FIG. 6. Ammonia nitrogen (μg/L) isopleths for experimental and control sides of Black Lake from 1978 to 1979.

was homogeneously distributed at 0.04−0.05 mg/L in October, and remained at this concentration throughout winter. All major ions examined (alkalinity, calcium, magnesium, and manganese) were significantly lower (two-way ANOVA, $P < 0.01$) throughout the experimental hypolimnion.

pH

Hypolimnetic aeration significantly increased (two-way ANOVA, $P < 0.01$) pH values on the experimental side. Epilimnetic values were not affected; however, hypolimnetic values were generally 0.1−0.4 pH units higher than corresponding control side values (Fig. 16). Fall circulation minimized pH differences between sides and homogeneous values persisted throughout winter.

Discussion

CIRCULATION

Circulation currents generated by the aerator had no effect on the formation and maintenance of thermal stratification throughout spring, summer, and early fall months. This indicates normal density stratification was sufficient to isolate the actively circulating hypolimnion (theoretical circulation time = 1.2 d) from the epilimnion with minimal danger of destratification or significant thermocline erosion.

Secchi disk and 1% transmission depths were similar on both sides when Secchi and 1% depths were less than 5 m. This suggests hypolimnetic circulation did not increase the vertical transfer of nutrients across the thermocline. Epilimnetic (0−5 m) nutrient data (total N and total P) confirm this hypothesis (Fig. 8, 11, and 12). A noticeable (>1 m) difference occurred when Secchi and 1% depths exceeded 5 m. Experimental depths were restricted to ~5 m (max. Secchi = 5.4 m, max. 1% = 5.2 m) whereas control depths were not restricted (max. Secchi = 7.0 m, max. 1% = 6.4 m) (Fig. 4).

I believe this difference was due to increased turbidity (detritus and Mn or Fe oxides) in the experimental hypolimnion (5−9 m) which was experiencing active circulation. Fast (1971) decreased the transparency of an oligotrophic lake because circulation currents kept detritus in suspension, and Ridley et al. (1966) observed decreased sedimentation of silt and organic debris in an English reservoir due to artificial circulation currents. Increased hypolimnetic turbidity may be a common feature of hypolimnetic aeration; however, this should not decrease epilimnetic transparency as circulation currents are confined to the hypolimnion during thermal stratification.

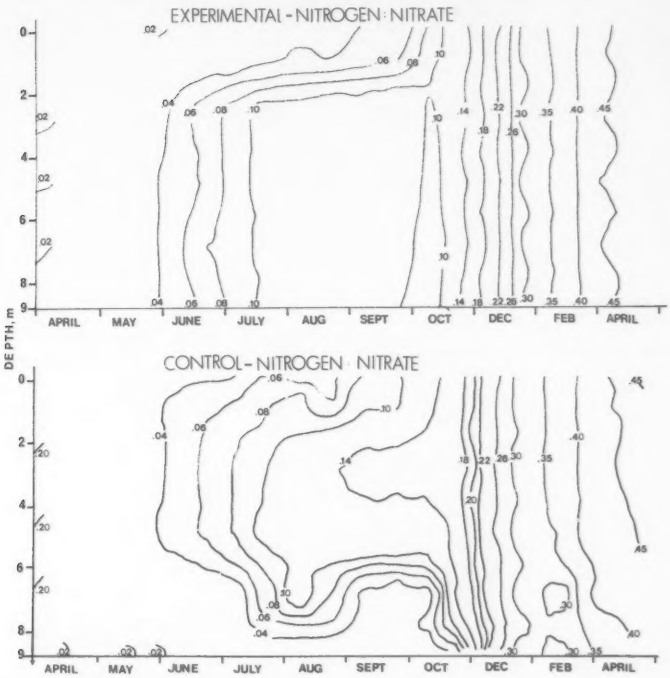

FIG. 7. Nitrate nitrogen (mg/L) isopleths for experimental and control sides of Black Lake from 1978 to 1979.

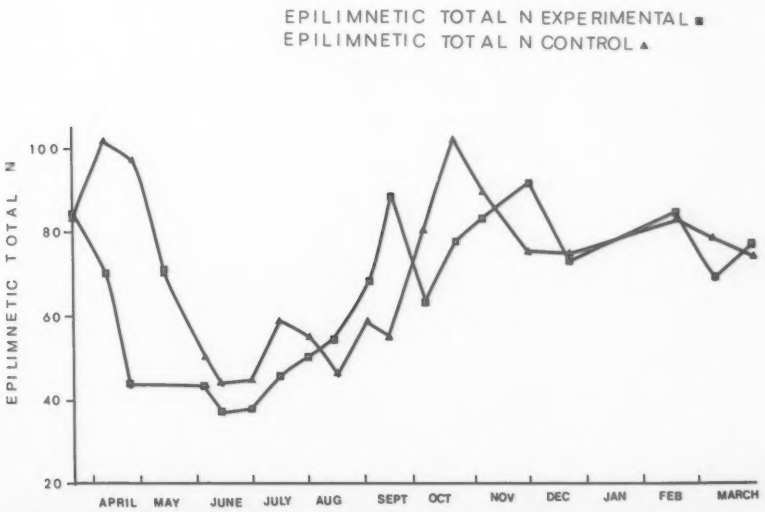

FIG. 8. Epilimnetic (0–5 m) total N (kg) in experimental and control sides of Black Lake from 1978 to 1979.

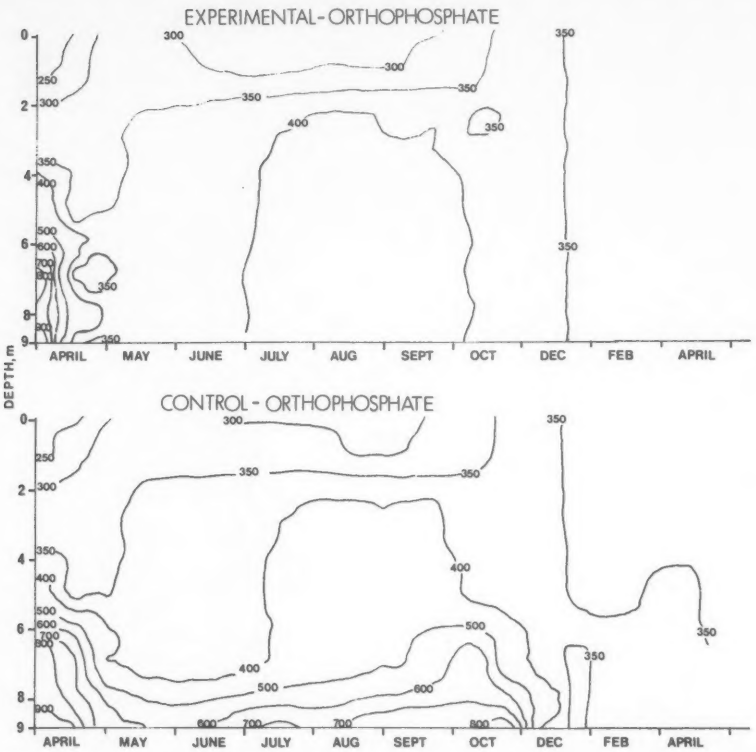

FIG. 9. Orthophosphate phosphorus (μg/L) isopleths for experimental and control sides of Black Lake from 1978 to 1979.

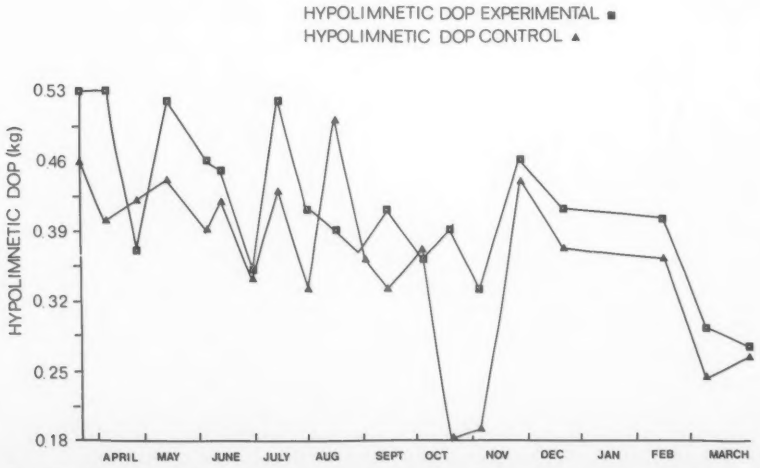

FIG. 10. Hypolimnetic (5–9 m) dissolved organic phosphorus (DOP) (kg) in experimental and control sides of Black Lake from 1978 to 1979.

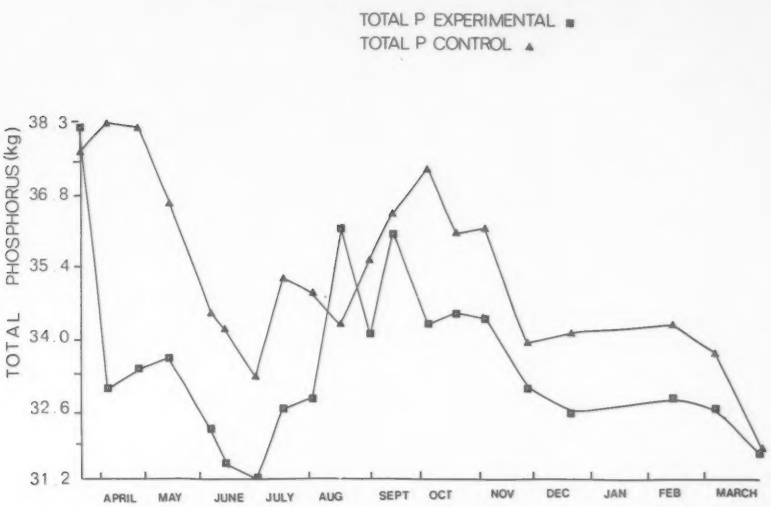

FIG. 11. Whole-lake total phosphorus (kg) in experimental and control sides of Black Lake from 1978 to 1979.

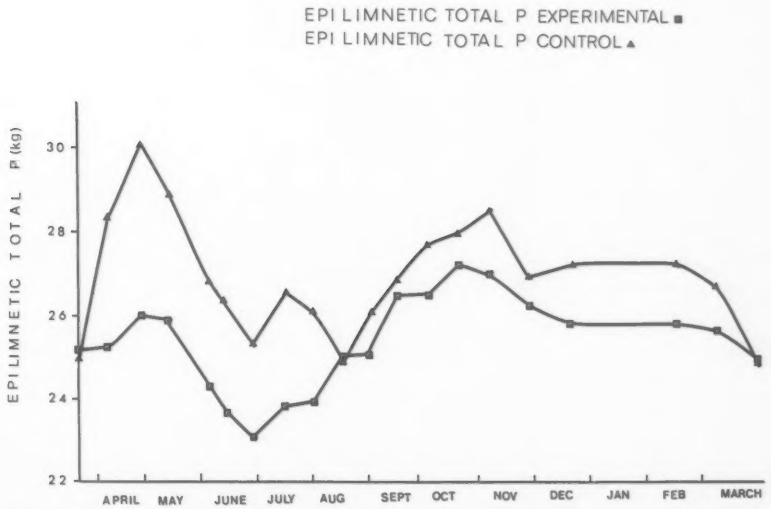

FIG. 12. Epilimnetic (0–5 m) total phosphorus (kg) in experimental and control sides of Black Lake from 1978 to 1979.

DECOMPOSITION

Experimental aeration significantly increased hypolimnetic oxygen concentrations and maintained aerobic conditions at the sediment–water interface throughout the year. However, hypolimnetic oxygen levels fluctuated within a narrow range (1.6–3.7 mg/L) (Fig. 5) all summer despite addition of 10.76 kg O_2/d by the aerator. I believe hypolimnetic aeration modified Black Lake decomposition processes in at least three ways.

First, circulation currents generated by the aerator stimulated sediment oxygen demand. In shallow eutrophic lakes the water column component of whole lake oxygen consumption is generally less than the sediment component due to accumulated organic material and bacterial populations at the sediment surface (Wetzel 1975). Sediment oxygen-uptake

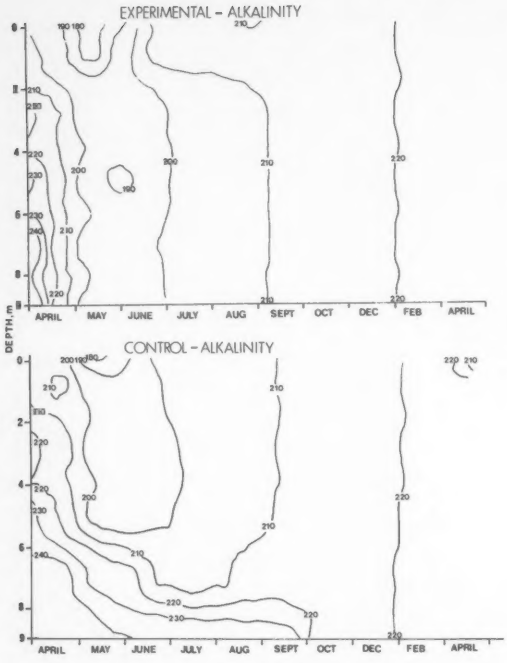

FIG. 13. Total alkalinity (mg/L) isopleths for experimental and control sides of Black Lake from 1978 to 1979.

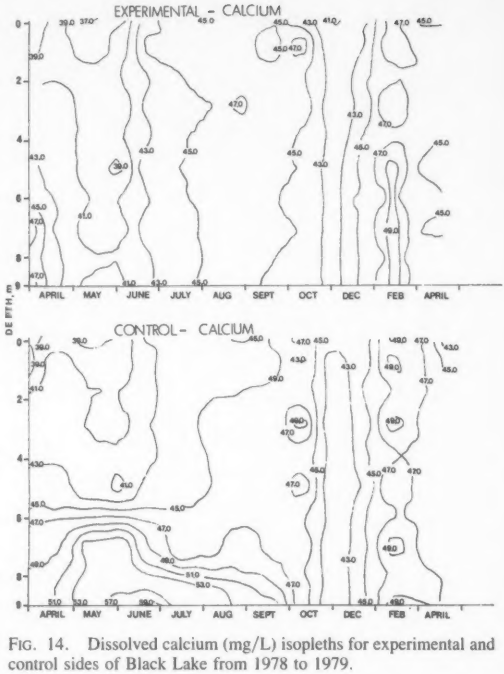

FIG. 14. Dissolved calcium (mg/L) isopleths for experimental and control sides of Black Lake from 1978 to 1979.

rates appear independent of oxygen concentrations in overlying waters when oxygen concentrations exceed 2–3 mg/L (Mathias and Barica 1980). However, when oxygen concentrations decline below 2–3 mg/L, oxygen uptake decreases as eddy diffusion is unable to overcome oxygen gradients at the sediment surface and the rate of oxygen supply becomes limiting (Mathias and Barica 1980). Artificial mixing markedly increases oxygen uptake at low oxygen levels (Hargrave 1969). Hypolimnetic aeration, by continually supplying the sediment–water interface with oxygen, prevented anaerobic conditions from developing and increased sediment oxygen consumption.

Second, continued suspension of sedimenting organic material (see Circulation) increased the water column component of hypolimnetic oxygen consumption. Once sedimenting detritus enters the hypolimnion of a shallow lake (e.g. Black Lake; max. depth = 9 m), it travels a relatively short distance before reaching the lake bottom. As a result, most decomposition occurs at the sediment surface, which in turn is often limited by insufficient oxygen. Hypolimnetic aeration increased the "effective depth" of the hypolimnion by circulating detritus and reducing settling rates, thus changing its function from a passive settling zone to an actively circulating decomposition zone. Sedimenting organic material then experiences more complete oxidation in the water column and the water column assumes greater importance as a decomposition zone in relation to the sediment surface (Charlton 1980). This process is analogous to increased depth of mixing in larger lakes which results in greater water column mineralization of organic material (Hargrave 1973, 1975).

The continued presence of oxygen should also stimulate the aerobic bacterial community in the hypolimnion. Organic substrate was readily available, and enhanced bacterial respiration should accelerate decomposition processes and increase oxygen consumption.

In summary, hypolimnetic respiration was not restricted by low oxygen levels and sediment-oriented decomposition, and consumed oxygen at its maximum temperature-dependent rate. Mass balance analysis confirms this assumption as experimental consumption was about an order of magnitude higher (0.39–0.78 $mg \cdot L^{-1} \cdot d^{-1}$) than control side values (0.03–0.09 $mg \cdot L^{-1} \cdot d^{-1}$) (Table 2). As the aerator supplied more oxygen, the sediments and water column consumed more oxygen. As the aerator was physically unable to exceed the additional oxygen demand, the system oscillated about a narrow range (1.6–3.7 mg/L) all summer. Literature values for threshold oxygen values (concentrations at which oxygen becomes limiting) (2–3 mg/L; Hargrave 1969, Mathias and Barica 1980) are close to the observed values in the aerated hypolimnion which suggests oxygen supply and demand were closely matched.

Oxygen concentrations increased at fall circulation as the entire lake was mixed, and experimental winter oxygen concentrations ranged between 6 and 7 mg/L. Temperature strongly influences seasonal variations in sediment oxygen

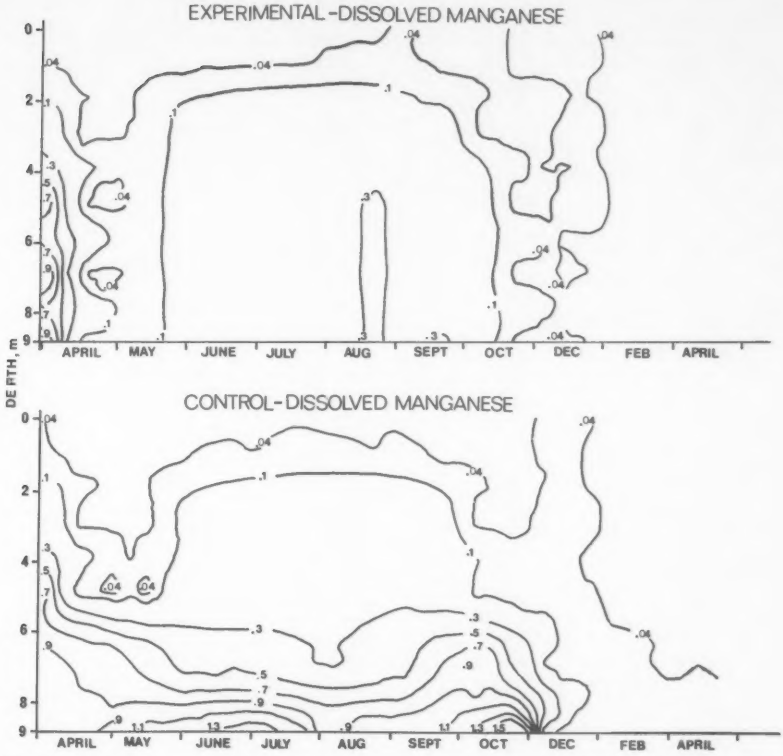

FIG. 15. Dissolved manganese (mg/L) isopleths for experimental and control sides of Black Lake from 1978 to 1979.

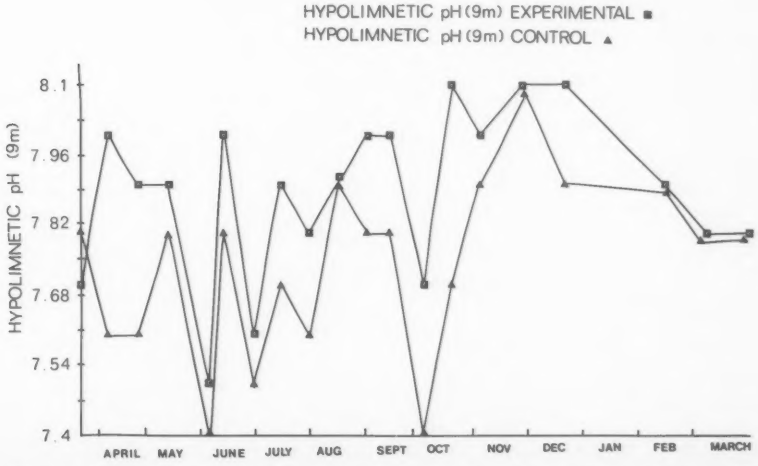

FIG. 16. Hypolimnetic (9 m) pH values for experimental and control sides of Black Lake from 1978 to 1979.

uptake (Hargrave 1969), therefore increases in winter oxygen concentrations were probably related to decreased sediment and water column consumption. Winter oxygen depletion rates were generally lower than summer rates. Graneli (1978) reported sediment Q_{10} (increase in metabolic rate per 10°C rise) values of 2.0−3.0 for the interval 5−10°C. This approximates observed differences in oxygen and temperature values on the experimental side between summer and winter (oxygen 1.6−3.7 mg/L summer, 6−7 mg/L winter; temperature 8−12°C summer, 2−3°C winter), and suggests that despite winter oxygen concentrations, supply and demand remained closely balanced.

Major Nutrients

Nitrogen — The nitrogen cycle was influenced by hypolimnetic aeration as hypolimnetic ammonia decreased dramatically after just 2 wk aeration. This was the result of several interacting processes. An unknown amount of NH_3-N escaped directly to the atmosphere when hypolimnetic water circulated through the separation box. Elevated hypolimnetic pH values (see pH and major ions) encountered during aeration facilitated this reaction by shifting the ammonia (NH_4^+)−(NH_3) equilibria toward the gaseous form (NH_3) which is more easily volatilized during vigorous bubbling (Stratton 1969). Increased hypolimnetic oxygen concentrations would also enable nitrifying bacteria to oxidize NH_3-N to NO_2-N and NO_3-N thereby reducing NH_3-N levels (Brezonik et al. 1969). In addition, the presence of dissolved oxygen at the lake bottom may have oxidized the surficial sediment layer and reduced NH_3-N release (Graetz et al. 1973).

The nitrification process was influenced by hypolimnetic aeration. The overall nitrification reaction occurs above an oxygen concentration of 0.3 mg/L:

$$NH_4^+ + 2O_2 \rightarrow NO_3^- + H_2O + 2H^+$$

(Wetzel 1975). Surface nitrate on both sides was below detectable levels (<0.02 mg/L) during the first weeks of aeration. Hypolimnetic nitrate on the experimental side did not appear immediately despite sufficient oxygen and a dramatic decline in NH_3-N. This suggests that most of the NH_3-N present on April 11 was volatilized and little converted to NO_2-N or NO_3-N. Murphy and Brownlee (1981) also observed rapid ammonia volatilization from prairie lakes when strong breezes accompanied elevated pH and NH_3-N levels. Hypolimnetic NO_3-N eventually appeared on June 13 and gradually accumulated during the summer months. Control side hypolimnetic NO_3-N (8 + 9 m) remained low all summer as insufficient oxygen was present for nitrification reactions to occur.

Fall circulation introduced substantial quantities of oxygen to both sides and a clearly defined nitrification sequence was again observed. After several weeks of circulation NO_2-N was replaced by NO_3-N which then accumulated throughout winter. Experimental evidence suggests that NO_3-N will not continue accumulating under aerobic conditions as NO_3-N diffuses into lake sediments (which are anoxic beneath the surficial layer) and is lost via denitrification or immobilization (Chen et al. 1979).

The implications of these results are wide ranging. Unionized ammonia (NH_3) is highly toxic to most aquatic organisms and becomes increasingly so at low oxygen concentrations (Merkens and Downing 1957; Thurston et al. 1981). Hypolimnetic aeration reduced hypolimnetic ammonia concentrations while increasing dissolved oxygen concentrations. This process should benefit the aerobic community in the hypolimnion. Although the concentration of toxic unionized ammonia (NH_3) increases with pH (Trussel 1972), the overall decline in total NH_3-N ensured un-ionized ammonia levels did not exceed recommended chronic exposure levels for fish (E.I.F.A.C. 1970).

The presence of increased NO_3-N in the aerated hypolimnion may enhance oxidation of bottom sediments. Ripl (1976) reported a novel technique for in situ oxidation of nutrient rich organic sediments via nitrate injection and subsequent denitrification (with nitrogen released to the atmosphere):

$$2NO_3^- + 3CH_2O \rightarrow N_2 + 3CO_2 + 3H_2O.$$

Andersen (1977) also discovered water column addition of nitrate enhanced organic matter degradation in lake sediments through denitrification. Therefore hypolimnetic aeration, by adding oxygen and stimulating nitrification, may enhance sediment oxidation in eutrophic lakes.

Nitrogen might also be removed from eutrophic lakes by alternating periods of hypolimnetic aeration and restratification to effect a nitrification−denitrification sequence. This procedure has been proposed for sewage treatment plants (Brezonik 1973) and may result in significant N removal from lakes (Chen et al. 1979).

Phosphorus — The immediate effect of experimental aeration was a large decline in hypolimnetic PO_4-P. I believe that most PO_4-P coprecipitated with calcium carbonate (calcite) which formed during the initial stages of aeration (see pH and major ions). This hypothesis is supported by the following observations. Phosphorus has been shown to coprecipitate with calcium carbonate in laboratory experiments (Otsuki and Wetzel 1972), and increased coprecipitation rates were observed under continuous mixing conditions. The pH rise in the experimental hypolimnion and turbulence in the aeration tube may have been sufficient to initiate this reaction. T. P. Murphy (NWRI, Burlington) has independently observed natural and experimentally induced abiotic calcite−phosphorus coprecipitation in Black Lake (Murphy et al. 1983) and concluded "the subsequent disappearance of phosphate was correlated with an increase in pH and a reduction of Ca and alkalinity and not necessarily with primary production or algal biomass." Rossknecht (1980) has also observed natural and experimental calcite−phosphorus coprecipitation in Lake of Constance (Obersee) and noted that the reaction kinetics of precipitation depends on the surface available for crystal growth in addition to the degree of calcium carbonate supersaturation. The increased hypolimnetic turbidity in Black Lake may have increased the available surface area for crystal growth and enhanced the coprecipitation reactions. In addition, some PO_4-P may have adsorbed onto

particulate detritus circulating in the hypolimnion.

Although ferrous–ferric iron complexes are directly involved with phosphorus release and precipitation reactions in redox-sensitive sediments (Mortimer 1971), dissolved iron concentrations in Black Lake were consistently below 0.1 mg/L (Ashley 1981) and appeared too low to account for the decline in hypolimnetic phosphorus. Reduced manganese (Mn^{+2}) was present initially; however, oxidized manganese compounds do not coprecipitate with PO_4-P (Hutchinson 1957), and despite their association with Fe complexes it is unlikely that Mn precipitation contributes significantly to PO_4-P accumulation in lake sediments (Syers et al. 1973).

The experimental treatment resulted in gradually increasing PO_4-P and higher concentrations of DOP and PP in the experimental hypolimnion during summer months despite aerobic conditions at the sediment–water interface. I believe this was a result of two processes: (1) aerobic P release from the sediments and (2) increased water column suspension and mineralization of sedimenting detritus. Although Mortimer's (1941–42) classic work is usually cited as evidence that P release is absent under aerobic conditions, Schindler et al. (1977, 1980) states Mortimer's views have become too widely extrapolated by limnologists, and that P release is influenced by a variety of factors including lake type, sediment composition, and historical nutrient loading in addition to oxygen concentrations at the sediment–water interface. Burns and Ross (1970) recorded 25% P regeneration from an aerobic hypolimnion (Lake Erie), and suggested most PO_4-P produced by organic decomposition is in close proximity to precipitated ferric hydroxides in the oxidized sediment microzone. This would lead to formation of insoluble ferric–hydroxyphosphate complexes and may partially explain the hypolimnetic accumulation of P under aerobic conditions.

Hypolimnetic aeration also increased hypolimnetic P concentrations by reducing detrital sedimentation rates and allowing for more decomposition in the water column which should have been relatively free of ferric hydroxide–phosphate complexes. As a result, hypolimnetic PO_4-P, dissolved organic P, and particulate P concentrations accumulated during summer despite aerobic conditions. Higher sediment temperatures and increased organic loading would also contribute to P accumulation. However, total P concentrations (epilimnion and whole-lake) remained lower on the experimental side. This suggests hypolimnetic aeration reduced internal phosphorus loading which is a primary goal of lake restoration projects where internal loading is a major P source.

pH and Major Ions

Experimental aeration vented accumulated carbon dioxide from the hypolimnion. Although escaping gas was not analyzed for CO_2 content, its removal was inferred from several sources. Aeration of water for CO_2 removal is common practice in water treatment engineering (Sawyer and McCarty 1978), and vigorous bubbling within the aerator was effective in venting hypolimnetic gases as evidenced by the rapid removal of accumulated NH_3. The calculation method of Rainwater and Thatcher (1960) also indicates experimental hypolimnetic CO_2 decreased from 10.2 to 4.2 mg/L in the first 2 wk of aeration whereas control (9 m) CO_2 increased from 7.8 to 12.5 mg/L.

Since CO_2 is an acidic gas, its removal to the atmosphere increased hypolimnetic pH 0.1–0.4 units according to:

$$CO_2 + H_2O \leftarrow H_2CO_3 \leftarrow HCO_3^- + H^+$$

(Sawyer and McCarty 1978). This shift was responsible for a number of important reactions, including ammonia volatilization as was previously discussed. For example, Ca^{+2}, Mg^{+2}, and HCO_3^- precipitated as carbonates. $CaCO_3$ precipitation in natural waters can be represented by two reactions (Otsuki and Wetzel 1974):

$$(1)\quad Ca^{+2} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$$

$$(2)\quad Ca^{+2} + CO_3^{-2} \rightarrow CaCO_3.$$

Reaction 1, in conjunction with CO_2 removal, increases pH values whereas reaction 2 decreases pH. Because bottom pH values increased during aeration, reaction 1 is the equation explaining $CaCO_3$ precipitation. The subsequent coprecipitation reaction results from the formation of a calcium–carbonate–phosphate surface complex:

$$3CaCO_3 + H_3PO_4 \rightarrow Ca_3(HCO_3)_3PO_4$$

(Avnimelech 1980).

Magnesium ions are chemically and biologically more conservative than calcium ions in natural systems (Wetzel 1975). Despite this conservative nature, magnesium concentrations decreased in response to hypolimnetic aeration. This is an unusual result because magnesium compounds are more soluble than calcium compounds and precipitate only at high pH (>10) values (Wetzel 1975). The pH increase in the aeration tube (although not measured) must have been considerably higher than the hypolimnion increase because the sediments would buffer any pH change. Fast et al. (1973) observed a similar decline during hypolimnetic aeration of a small hardwater lake. Therefore I suggest magnesium precipitated in conjunction with $CaCO_3$, possibly as $CaMg(CO_3)_2$.

These conclusions are based on several observations. Solubility product calculations indicate that both $CaCO_3$ and $CaMg(CO_3)_2$ precipitation could occur under these conditions. Dissolved calcium, magnesium, and bicarbonate concentrations in the experimental hypolimnion declined significantly after just 13 d aeration and remained lower throughout thermal stratification. Finally, analysis of sediment samples (n = 2, upper 10 cm) taken April 15, 1979, at 8 m revealed calcium concentrations of 31.3 mg/g (dry wt) on the control side and 43.0 mg/g (dry wt) on the aerated side. After the initial precipitation reaction aerobic conditions in the experimental hypolimnion maintained lower bicarbonate, calcium, and magnesium concentrations by preventing anaerobic release of bicarbonates and dissolution of precipitated $CaCO_3$.

Major ion reactions initiated by hypolimnetic aeration were analogous to epilimnetic reactions caused by intense algal activity in eutrophic hardwater lakes, i.e. increased pH, decreased CO_2, and Ca^{+2} and $CaCO_3$-PO_4 coprecipitation. I am unaware of any hypolimnetic aeration study reporting

similar results, although Fast (1971) and Taggart and McQueen (1981) have postulated the existence of these reactions. Wetzel (1975) suggests that $CaCO_3$ precipitation is a major sink for inorganic and organic carbon and states "Elevation of the pH of water containing typical concentrations of calcium should lead to apatite formation." Otsuki and Wetzel (1972) reported coprecipitation of phosphate ions with $CaCO_3$ as pH increased, and indicated this may function as a population control mechanism for primary producers. Rossknecht (1980) estimates calcite–phosphorus coprecipitation removed 90–130 t of phosphorus from the epilimnion of Lake of Constance during periods of intense primary production. Therefore hypolimnetic aeration should ultimately reduce phosphorus concentrations in eutrophic hardwater lakes by calcite coprecipitation and enhance the restoration of these lakes.

The effect of hypolimnetic aeration on manganese distribution was striking. Brezonik et al. (1969) reported oxidation of soluble Mn^{+2} to particulate manganese oxides and its subsequent precipitation during destratification of Cox Hollow Lake, Wisconsin. Previous hypolimnetic aeration experiments have also reported lower Mn^{+2} concentrations following aeration (Bernhardt 1967, 1974). Divalent manganese has caused major fish kills in hatcheries (Ingols 1975) and hypolimnetic aeration of the water supply lake should eliminate this problem.

In concluding, hypolimnetic aeration exerts a greater influence on the lake ecosystem than was previously realized. Subtle shifts in pH catalyzed a number of chemical reactions including ammonia volatilization, calcium, magnesium, bicarbonate, and phosphorus precipitation. Hypolimnetic aeration is not just a cosmetic treatment for increasing low oxygen concentrations (Dunst et al. 1974), but a useful technique for manipulating lake ecosystems.

Management implications of this study are obvious. One should now be able to control the concentration of nitrogen and phosphorus and type of nitrogen (e.g. NO_3 or NH_3) in the hypolimnion. This should lead to a long-term decline in internal nutrient loading and should reverse eutrophication in lakes characterized by excessive internal loading. pH shifts could be used to precipitate divalent metallic cations and improve hypolimnetic hardness and water quality for domestic use. Fisheries applications include winterkill prevention in temperate lakes (Fast 1971) and creation of "two-storey" fisheries in warmer climates. The aeration equipment could also be used to improve the effectiveness of other lake restoration techniques such as hypolimnetic alum and nitrate applications.

Acknowledgments

I thank F. A. Ashley and G. T. Ozone Sutherland for field and technical assistance throughout this project. C. J. Bull, D. McKay, D. Smith, Dr A. F. Tautz and K. Tsumura were helpful on a continuous basis. Drs D. W. Schindler, T. G. Northcote, and D. C. Lasenby provided valuable comments and criticisms of the manuscript. This study was supported by the Fisheries Research Section of the British Columbia Fish and Wildlife Branch (Ministry of Environment) and an NRC grant (67-3454) to Dr T. G. Northcote.

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An Arctic Intertidal Population of *Macoma balthica* (Mollusca, Pelecypoda): Genotypic and Phenotypic Components of Population Structure

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GREEN, R. H., S. M. SINGH, B. HICKS, AND J. M. MCCUAIG. 1983. An arctic intertidal population of *Macoma balthica* (Mollusca, Pelecypoda): genotypic and phenotypic components of population structure. Can. J. Fish. Aquat. Sci. 40: 1360–1371.

In July 1980 we collected live *Macoma balthica* from populations at two tide levels near Fort Churchill, Man., Canada. Upper lethal temperature tolerances were determined for clams from the mean low water (MLW) tidal level and from 1.1 m above MLW tidal level, after which all specimens were hard frozen for later electrophoretic analysis. Of 22 loci evaluated, the following were polymorphic: AKP, ACP, EST, LAP, MDH, and ME. Genotypes at these loci were related to tide level, growth rate, tolerance to high temperature, and age. Analysis of shell annual rings verified an earlier report of much faster growth in the higher tide level population. Growth rate and degree of heterozygosity are both higher at 1.1 m than at MLW. Degree of heterozygosity increases with age, suggesting selection against homozygotes. At 1.1 m, but not at MLW, individuals with higher growth rates have lower tolerance to high temperatures and a higher degree of heterozygosity. Similar patterns are described for the six individual loci.

GREEN, R. H., S. M. SINGH, B. HICKS, AND J. M. MCCUAIG. 1983. An arctic intertidal population of *Macoma balthica* (Mollusca, Pelecypoda): genotypic and phenotypic components of population structure. Can. J. Fish. Aquat. Sci. 40: 1360–1371.

Nous avons prélevé des spécimens vivants en juillet 1980 de populations de *Macoma baltica* à deux niveaux de marée près de Fort Churchill (Manitoba, Canada). Les températures létales supérieures ont été déterminées pour les myes peuplant la zone de basse mer moyenne (BMM) et la zone située à 1,1 m au-dessus du niveau de BMM. Les spécimens ont ensuite été congelés pour fins d'analyse électrophorétique. Des 22 loci étudiés, les suivants étaient polymorphiques: AKP, ACP, EST, LAP, MDU et ME. À ces loci, les génotypes étaient en rapport avec le niveau de la marée, le taux de croissance, la tolérance aux températures élevées et l'âge. L'analyse des zones annuelles des oreillettes a confirmé une étude précédente selon laquelle la croissance est plus rapide chez la population habitant la zone de plus haute marée. Le taux de croissance et le degré d'hétérozygotie sont plus élevés dans la zone située à 1,1 m au-dessus du niveau de BMM. Le degré d'hétérozygotie augmente avec l'âge, ce qui porte à croire à une sélection contre les homozygotes. À 1,1 m, les individus au taux de croissance supérieur tolèrent moins des températures élevées et possèdent un plus haut degré d'hétérozygotie, ce qui n'est pas le cas chez les spécimens peuplant la zone de BMM. Le rapport décrit des schèmes semblables pour les six loci individuels.

Received October 29, 1982
Accepted May 18, 1983

Reçu le 29 octobre 1982
Accepté le 18 mai 1983

IN a report of studies conducted (during 1970 and 1971) in an intertidal community on Hudson Bay near Fort Churchill, Green (1973) described a higher growth rate for *Macoma balthica* living at a tidal level of 1.1 m above mean low water (MLW) than those at the MLW level. It was concluded that temperature, especially summer air temperatures which mainly affect the higher tidal level *Macoma* during daytime low tides, is probably responsible. In this paper we investigate relationships (both between and within the two tidal level subpopulations from the same community) among growth rate, tolerance to high temperature, and genetic factors.

Printed in Canada (J7100)
Imprimé au Canada (J7100)

SYSTEMATICS AND BIOLOGY

Macoma balthica is a tellinid bivalve mollusk, widely distributed in temperate, boreal and arctic shallow waters of the North Atlantic, and a characteristic species of brackish waters (e.g. Chesapeake Bay, the Baltic Sea, southern Hudson Bay). Larval and postsettlement stages are distinct, and there is synchronous spawning and external fertilization. The species has been studied extensively. Studies on subtidal populations include Chesapeake Bay (McErlean 1964); North Sea and Baltic Sea (Vogel 1959; Segerstråle 1960, 1973, 1978). Studies on intertidal populations (in some cases overlapping into the subtidal) include Connecticut (Levinton 1973);

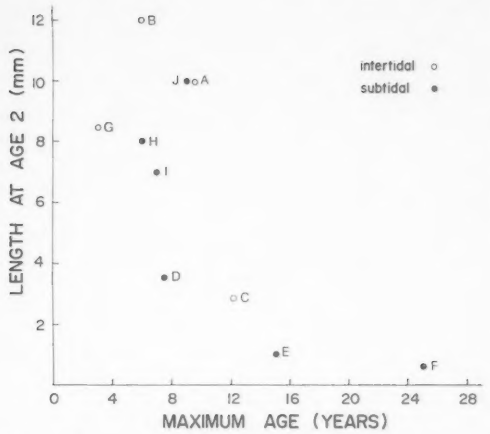

FIG. 1. Summary of information on growth rate and longevity of *Macoma balthica*. Geographic locations and literature sources are A: Hudson Bay near Churchill, at 1.1-m tidal level (Green 1973); B: Netherlands (Lammens 1967); C: St. Lawrence River estuary (Lavoie et al. 1968); D, E, and F: Tvärminne at 3, 20, and 35-m depth, respectively (Segerstråle 1960); G: Scotland (Stephen 1931); H: Kiel (Vogel 1959); I and J: Tvärminne and North Sea, respectively (Vogel 1959).

Massachusetts (Sanders et al. 1962); St. Lawrence River estuary (Lavoie et al. 1968); Bay of Fundy (Tunnicliffe and Risk 1977); England (Brafield and Newell 1961; Newell 1965); Scotland (Stephen 1931); Netherlands (Lammens 1967; Swennen 1969); Norway (Strömgren et al. 1973); West Greenland (Petersen 1978).

Available information on growth and longevity is summarized in Fig. 1; the inverse relationship between growth rate and lifespan mentioned by Segerstråle (1960) is apparent. Depth is certainly a factor in the Baltic, which suggests temperature and perhaps also available food for deposit feeders. Higher temperatures in shallower waters may increase growth rate, but a risk of lethal high temperatures is suggested by the fact that populations are intertidal only in colder climates (see above references). Bivalve species in general tend to become more intertidal and then higher intertidal toward the northern parts of their ranges along the northwest Atlantic coast (Green and Hobson 1970). Mass mortalities related to extreme temperatures during summer afternoon low tides have been described for intertidal bivalve populations on the mid-Atlantic U.S. coast (e.g. Sellmer 1967), where those populations are just becoming intertidal in contrast to all-subtidal populations of the same species further south. Where northern populations of *M. balthica* are entirely subtidal it is usually because there is no intertidal zone (e.g. the Baltic Sea) or because harsh climatic conditions made that zone uninhabitable. At Fangsthytten, West Greenland, Petersen (1978) found *M. balthica* predominately in the brackish water zone shallower than 6 m including the intertidal (replaced in deeper high salinity water by *M. calcarea*), whereas at Cape Hatt, N.W.T. (north Baffin Island) where the intertidal is mostly rock, ice-scoured, and flooded in spring with near-fresh water, only subtidal fauna which includes *M. calcarea* but not *balthica* are found (Cross and Thomson 1981).

Lower salinity depresses growth rate (Vogel 1959; Segerstråle 1960) although *M. balthica* does better in brackish waters than most of its marine bivalve associates including such congeners as *M. calcarea*. A reported exception, of reduced *M. balthica* size at higher salinities, is by McErlean (1964) for the lower Patuxent River (Chesapeake Bay). In Hudson Bay, where our work has been done, Lubinsky (1958) found that reduced growth rate of *Mytilus edulis*, which also intrudes into brackish waters, was associated with lower salinities. A similar study on Hudson Bay *M. balthica* was, unfortunately, not done. Despite colder water, winter ice scour, a salinity of only 18‰, and an ice-free season averaging only 104 d (Fig. 2 and 3; Green 1973 Table 1), *M. balthica* growth rates at the 1.1-m tidal level at Churchill are comparable to those reported for Scotland (Stephen 1931) and the Netherlands (Lammens 1967).

Available food as a factor influencing growth rates is difficult to assess because trophically *M. balthica* is a classic jack-of-all trades. As described by Brafield and Newell (1961) and Newell (1965), it is a facultative filter-feeder/surface film deposit-feeder. When deposit-feeding it is mainly using microorganisms which are breaking down refractory organic material and which are more abundant in fine than in coarse sediments (Dale 1974) because of the greater particle surface area. Tunnicliffe and Risk (1977) found *M. balthica* density to be correlated with bacterial density rather than with organic content of sediment (Minas Basin, Bay of Fundy). They also determined that both suspension-feeding and deposit-feeding were necessary for minimum protein requirements to be met. Because sediments tend to be finer low rather than high in intertidal environments, and water cover allowing filter-feeding is of longer duration there, it might be expected that food availability would generally be greater as well. It is difficult to make a case for food availability as a factor responsible for the higher growth rate at 1.1 m than at MLW at Churchill (Green 1973), except indirectly by higher ambient temperature causing a higher feeding rate. Strömgren et al. (1973) studied a Norwegian fjord intertidal population of *M. balthica* which had peak densities of 200−300 m^{-2} at a height of ~50% exposure/submergence (*M. calcarea* was present at and below MLW only), and where growth to 8−10 mm length in 2 yr was estimated (compare with Fig. 1). No estimate of longevity was given. The authors suggested a relationship between growth rate and available food, but also stated that "During summer the temperature on the beach may be fairly high" and therefore "Good growth conditions may be assumed." Among localities, temperature and organic content of sediments were positively correlated with each other and with higher growth rates. Within localities they found a consistent pattern of larger individuals (suggesting higher growth rates) at lower levels on the shore, which is the opposite of our results (Green 1973; this study).

Feeding behavior can be modified by trematode infestation (Swennen 1969) which is probably more prevalent higher on the shore where the avian primary hosts most often feed and defecate. However, *M. balthica* escapes other parasites such as athecate hydroids which can infest deeper-water higher-salinity congeners and reduce their growth rates (Petersen

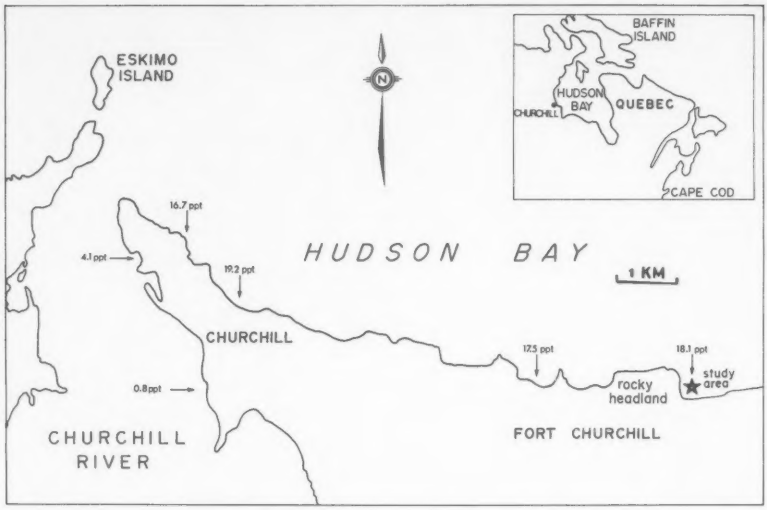

FIG. 2. Study area, showing surface salinity values (ppt = ‰) at high tide on July 9, 1970.

1978). No doubt there is also size-selective predation by both fish and shorebirds. For example, Goss-Custard et al. (1977) found that oyster catchers feed heavily on small shellfish, including *Macoma*, and that "they select large *Macoma* -- and only take other size classes in large numbers when the preferred ones are scarce."

GENETIC FACTORS

Previous genetic work by Levinton (1973) on *M. balthica*, and on eight other *Macoma* species on the Pacific coast (Levinton 1975), indicated that the LAP and PGI loci were polymorphic and that there were varying degrees of excess homozygosity (in comparison with the expectation from the Hardy–Weinberg equilibrium). Possible relationships to salinity or temperature variation were suggested. Levinton and Fundiller (1975) described variation in allele and genotype frequency at the LAP locus, as a function of both tidal height and organism size, for *Mytilus californianus*. Salinity-related differences at the LAP locus among populations of *M. edulis* were described by Koehn et al. (1980). Singh and Zouros (1978), Zouros et al. (1980), and Singh (1982) have described excess homozygosity in cultured populations of *Crassostrea virginica*, and a positive correlation between growth rate and degree of heterozygosity at five polymorphic loci. Singh and Green (1983) reviewed this area and discussed our genetic results in relation to the biological significance of excess homozygosity in marine mollusks. Koehn and Shumway (1982) provide experimental evidence that in oysters the more heterozygous individuals have lower oxygen consumption rates, and that the most homozygous individuals sustain a metabolic cost twice as great as the most heterozygous individuals.

In summary, *M. balthica* can withstand extremes of salinity and temperature and is therefore a dominant species in brackish waters, which few other marine species can occupy (Remane 1934; Hedgpeth 1957b), and at midintertidal levels where storms as well as temperature extremes can cause mass mortalities (Yeo and Risk 1979). Low salinities reduce growth rate, whereas higher temperature increases growth rate but with increasing risk of heat stress during summer low tides.

Study Area

The *M. balthica* population studied by us in 1970, 1971, and 1980 is on a mixed sand and boulder beach 7 km east of Churchill on Hudson Bay at latitude 58°46′N (Fig. 2). Nearshore surface water salinities are ~18‰. The annual climatic cycle is summarized in Fig. 3. Mean high-tide water-surface temperatures in the mouth of the Churchill River for July, August, September, and October 1971 were, respectively, 2.1, 2.2, 5.0, and 3.9°C. The mean tidal range is 3.35 m (Fig. 4), and in winter broken ice piles up on shore and scours the intertidal zone. Tops and upper sides of boulders are scraped clean; attached organisms (e.g. *Fucus* and *Mytilus*) are found only on the undersides. The *Macoma* subpopulations on sand flats at MLW and at 1.1 m above MLW are separated by an ~200-m-wide rock reef and tide pool system, which makes it unlikely that adult *Macoma* could move between these tidal levels. The sand is finer at MLW than at 1.1 m above MLW (Fig. 5).

Methods

FIELD METHODS

At the end of July 1980, on the best summer low tide, we collected large and approximately equal numbers of *M. balthica* from the MLW and the 1.1-m tidal level sand

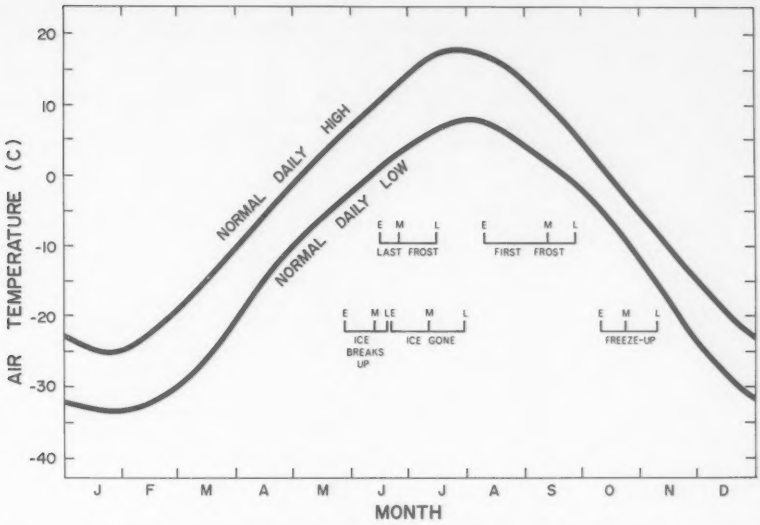

FIG. 3. The annual climatic cycle at Churchill, Manitoba, Canada. The data are for the period 1928–61, and are taken from a chart prepared by the Canada Department of Transport, and from the 1969 Report of the Royal Commission Inquiry into Northern Transportation, Province of Manitoba.

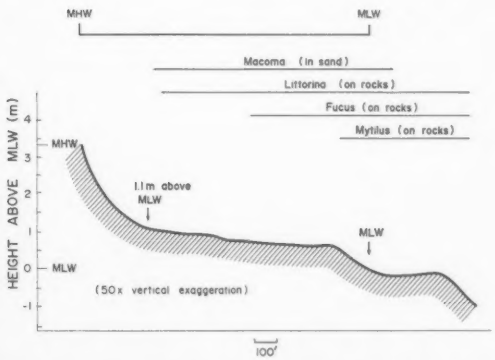

FIG. 4. The intertidal zone in profile, with the ranges of four species.

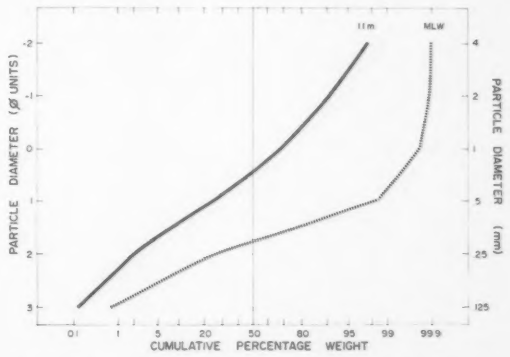

FIG. 5. Particle-size distributions of sediment at the two tidal levels.

flats. Collection was by hand, and we attempted to collect a wide range of sizes of clams from each tidal level rather than to sample randomly with respect to size. However, it was obvious that clams were smaller at MLW and that the rings on the shell surface were more closely spaced. Our collection reflects this. The clams were bagged with wet *Fucus* and kept on ice until they were returned to London, Ont., 36 h later and placed in Instant Ocean tanks at ~4°C. All experiments on the live *M. balthica* were carried out over the next 2 d, during which time there was negligible mortality in the holding tanks. Therefore, differential mortality among genotypes, after collection, does not influence our results.

PHYSIOLOGICAL METHODS

Lethal high temperature experiments were run as follows. An equal number of clams from each tidal level, covering the range of sizes as evenly as possible, were submerged in Instant Ocean seawater at each experimental temperature for 7 h. Mean clam size necessarily differed between clams from different tidal levels, as discussed above, but did not differ among experimental temperatures. Death was recorded when a gaping clam was prodded yielding no response. We have confidence in this criterion for death, because gaping was very definite and occurred abruptly. Response to touch was a

definite closure of the valves, or no response at all. Clams that were clearly gaping consistently showed no response to touch. Several gaping clams were returned to cold water and did not recover. Acclimation to high temperature was not attempted, and exposure time did not go beyond 7 h; given the tidal rhythm of exposure neither seemed biologically realistic. Immediately after death, or for survivors at the end of a 7-h exposure, each clam was blotted and weighed wet on a digital balance, its length was measured with vernier calipers, and then it was hard-frozen (−70°C) in an individual numbered vial.

Genetic Methods

Preliminary electrophoretic analyses on 22 loci determined that 6 were polymorphic: alkaline phosphatase (AKP), acid phosphatase (ACP), esterase (EST), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), and malic enzyme (ME). The tissue of each clam from temperature-tolerance experiments at 32, 33, and 34.5°C (see Results) was homogenized and the genotype at each of these six loci was determined. Electrophoretic methods followed Singh and Zouros (1978).

Methods for Determination of Growth Rate and Age

Lengths at annual winter shell rings were measured for each clam using vernier calipers. Thin sections of shells validated these external rings (Fig. 6). (Segerstråle (1960) confirmed the annularity of *M. balthica* shell rings in the Baltic Sea.) At higher magnification four to five finer internal bands (the number of lunar months during the ice-free season at Churchill) are visible between the annual winter rings.

Statistical Methods

Lengths in consecutive years were used to determine growth curves and ages for each tidal level, by the Walford plot method of Ford (1933) and Walford (1946) as used by Green (1973) and McCuaig and Green (1983). This approach represents the data as a "length next year (L_{t+1}) versus length this year (L_t)" bivariate plot. A linear relationship indicates that the von Bertalanffy model $L_t = L_\infty(1-e^{-Kt})$ applies (Bertalanffy 1934; Richards 1959; Kaufman 1981). If it is not linear then some other growth model, e.g. the Gompertz model, is required. A Walford Plot is simply a difference equation representation of the length-versus-age functional relationship, in general $L_{t+1} = f(L_t)$, and it can lead directly to tests of biological hypotheses by analysis of covariance. The slope and intercept parameters of the difference equation $L_{t+1} = a + bL_t$ have simple biological interpretations: a = the 1st year's growth, and b = the ratio of any given year's growth to the previous year's growth or, equivalently, the fraction of total growth remaining after the 1st year (see Green 1979; McCuaig and Green 1983). Kaufman (1981) feels that the lack of a simple identity between the Walford Plot parameters a and b and the von Bertalanffy parameters L_∞ (asymptotic maximum length) and K (instantaneous growth rate at $t=0$, expressed as a fraction of L_∞) is a serious problem. We disagree. The relationships $a = L_\infty(1 - e^{-K})$ and $b = e^{-K}$ are not complex, and the biological meaning of the parameters a and b themselves is straightforward. Because this approach uses for statistical analysis the original observations on lengths at annual winter rings, and because it lends itself to classical linear additive model statistical treatment, it is preferable to the various approaches based on index-type derived variables which have been commonly used in the past.

If the Walford Plot difference equation $L_{t+1} = a + bL_t$ is used, then a simple "growth rate index" for a particular clam, to describe its growth rate relative to other clams from the same sample, is the mean of vertical deviations of observed L_{t+1} values from the $\hat{L}_{t+1}$ values predicted by the Walford Plot least squares regression model. Such an index has a straightforward biological interpretation: deviation of that clam's mean annual growth from the average, given the same size at the beginning of the year. We have used this growth index here to describe variation in growth rate among clams, within each tidal level subpopulation.

We use analysis of covariance (Snedecor and Cochran 1980) to test hypotheses about differences between tidal levels in the parameters of regression lines. See McCuaig and Green (1983) for examples of analysis of covariance (ANCOVA) applied to Walford Plot data. The linear regression form of a one-way ANCOVA model, with the two tidal levels as the groups, is $Y = \beta_0 + \beta_1(X) + \beta_2(\mathrm{TL}) + \beta_3(\mathrm{TL}\cdot X) + \epsilon$. In the Walford Plot model, for example, $Y = L_{t+1}$ and $X = L_t$. The tide level code TL can be any two arbitrary values, but 0 and 1 are computationally convenient. (For more than two groups, additional dummy variables would be necessary.) Hypotheses are easily tested. If the null hypothesis "H_1: $\beta_3 = 0$" is rejected, then the linear regressions of Y on X have different slopes at the two tide levels. If H_1 is not rejected, then β_3 can be set to zero and rejection of "H_2: $\beta_2 = 0$" indicates parallel regression lines with differing intercepts. Interpretations of β_0 and β_1 have already been given for the Walford Plot model. The adequacy of a linear model can be tested by adding a term "$\beta_4(X^2)$" and testing "H_0: $\beta_4 = 0$". We did this routinely and found that H_0 could be accepted in every case, including the Walford Plot models.

It is assumed that the errors ϵ are normally and independently distributed and that X is measured without error. Tests are fairly robust to violations of assumptions if the design is balanced (i.e. approximately equal numbers of observations at each tidal level) and error degrees of freedom are large (Glass et al. 1972; Harris 1975); both are satisfied here. We have three concerns regarding the assumptions. One is that we are applying a Model I bivariate analysis to uncontrolled variables measured with error. See Glass et al. (1972) and Snedecor and Cochran (1980) for discussion of this problem. Increased error in the covariate (the predictor, or "independent," regression variable) leads to a bias downward in the estimate of the regression coefficient, and decreased power of the covariate to adjust the criterion, or "dependent," variable. This causes a conservative bias in tests (i.e. greater difficulty in rejecting null hypotheses of no relationship between variables, or of no difference in those relationships between tidal levels). We do find a small conservative bias in our estimates and tests (see Results).

The second concern is that in the Walford Plot analyses

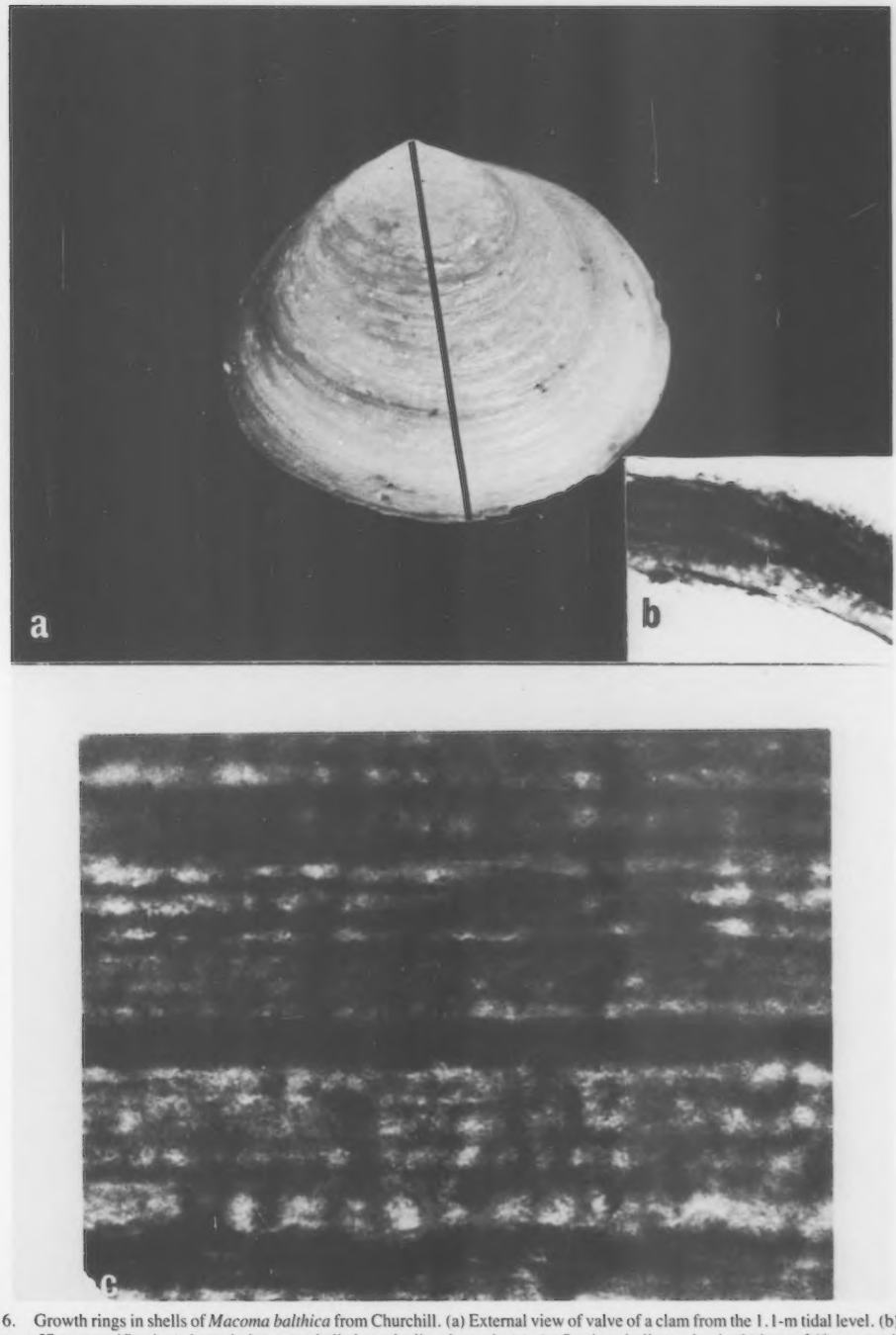

FIG. 6. Growth rings in shells of *Macoma balthica* from Churchill. (a) External view of valve of a clam from the 1.1-m tidal level. (b) Section (shown at 57 × magnification) through the same shell along the line drawn in (a). (c) Section similar to that in (b) but at 240 × magnification.

there is certainly some heterogeneity of residual error about the regression lines. Following Snedecor and Cochran (1980, p. 174) we determined the $S_{L_{t+1}}{}^2 = f(L_t)$ relationships, and applied both weighted and unweighted ANCOVAs to our Walford Plot data. Estimates of error and test statistics differed, but the same conclusions regarding levels of significance or nonsignificance were reached in all cases. As Mosteller and Wallace (1964) comment, it is "an old story in statistics that modest changes in weights ordinarily change the output modestly."

The third concern is serial correlation, of errors and of L_t values (Maddala 1977; Ostrom 1978). We expected negative serial correlation caused by our use of each "length at winter ring" measurement as an L_{t+1} value in one pair of values and as an L_t value in the adjacent pair. Negative serial correlation causes a conservative bias in tests because residual errors are overestimated. We also expected a positive serial correlation of L_t values, because of frequent sequences of L_t values from the same clam. From the Durbin–Watson statistic, χ^2 contingency table analysis of sequential errors, and serial correlation of L_t values, we determined that L_t values have some positive serial correlation ($r = 0.41$, $P < 0.01$), and that serial correlation of errors ranges from $r = -0.22$ ($P \approx 0.05$) to $r = 0.16$ ($P \approx 0.05$) depending on which error term is used for the particular test (rings within clams, or rings within and among clams). No liberal bias in tests was expected, but to be sure we analyzed the data with all "L_t, L_{t+1}" pairs, and then repeated the analysis with pairs deleted which contained L_t values previously used as L_{t+1} values. The same conclusions regarding levels of significance or nonsignificance were reached.

Our approach to statistical testing of intervariable relationships is a conservative one. First, the multivariate relationship among all the variables (listed above) is tested using Bartlett's sphericity test (Harris 1975), against the null hypothesis that all true correlations are zero. This is done both on a Pearson correlation matrix and on a Spearman's rho rank correlation matrix. Second, given rejection of the null hypothesis in both tests, we proceed to test the bivariate relationships (trivariate in the sense that each includes a test of differences between tidal levels) by analysis of covariance. Each bivariate relationship is also tested using Spearman's rank correlation, and the regression parameters a and b are reestimated using the RLINE ("resistant line") procedure (Ryan et al. 1981, after Mosteller and Tukey 1977). We accept only relationships for which the null hypothesis can be rejected in all tests.

Results

Growth Rates

A factorial analysis of covariance was done on the Walford Plot relationship $L_{t+1} = \alpha + \beta L_t$; tidal levels MLW and 1.1 were crossed in a 2 × 2 factorial design with years 1970 and 1980. There is a higher growth rate at the 1.1 m than at the MLW tidal level for both the 1970 and the 1980 samples (Fig. 7). Intercepts, but not slopes, differ between tidal levels ($P < 0.01$). The intercepts also differ ($P < 0.01$) between the years 1970 and 1980, with slower growth at both tidal levels in 1980; we have no explanation for this but it should

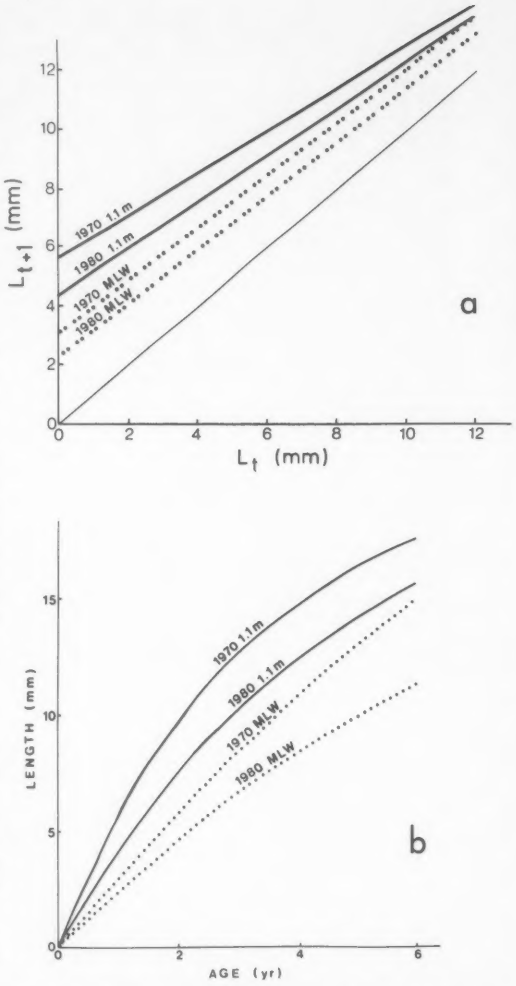

FIG. 7. (a) Least squares regression lines for Walford Plot of length (L) at one winter ring (year $t+1$) versus length at the previous winter ring (year t), for *Macoma balthica* sampled in 1970 and 1980 at the mean low water (MLW) and the 1.1 m above MLW tidal levels. (b) The von Bertalanffy growth curves corresponding to the Walford Plot regression lines.

be remembered that the populations were sampled in 1970 and 1980 whereas the growth we are analyzing occurred during periods, of several years duration, prior to those dates. There was no interaction between tidal level and years ($P > 0.05$), indicating that there is no evidence of any change over the intervening decade in the growth rate difference between the two tidal levels.

A hierarchical ANCOVA (annual ring pairs nested within clams which are in turn nested within tidal levels) indicated

TABLE 1. The matrix of correlations among five biological and environmental variables, based on 154 clams, and results of a principal component analysis on this correlation matrix. In the upper half of the matrix the correlations exceeding $r = 0.158$, the $\alpha = 0.05$ critical value, are underlined. The number of heterozygous loci can range from 0 to 6. There are two tidal levels, scored 1/2. Time-to-death is in hours, in the high lethal temperature experiment. The growth rate index measures within-tidal level growth rate variation, and should have no correlation with tidal level. Age in years is back-calculated from length, based on the growth model appropriate to that tidal level.

Variables	No. heterozygous loci	Tidal level	Time-to-death from heat stress	Growth rate index	Age
No. heterozygous loci	1.00	0.19	0.00	0.22	0.19
Tidal level	0.19	1.00	−0.04	0.03	0.13
Time-to-death from heat stress	0.00	−0.04	1.00	−0.10	0.03
Growth rate index	0.22	0.03	−0.10	1.00	0.14
Age	0.19	0.13	0.03	0.14	1.00

PC	Root	Vectors				
I	1.47	0.59	0.41	−0.09	0.47	0.50
II	1.05	0.09	0.20	0.85	−0.39	0.27
III	0.96					
IV	0.82					
V	0.70					
Sum	5.00					

that growth rates differ among clams within tidal levels ($P < 0.01$). Therefore, our growth rate index will be describing real variation in growth rate among clams from the same tidal level.

Relationships Among Growth, Environmental and Genetic Parameters

In the lethal high temperature experiments all clams survived for 7 h at 20, 24, and 28°C. At 36°C all died within a few minutes. In the 32, 33, and 34.5°C experiments time-to-death (TTD) was distributed throughout the 7-h period (the estimated incipient lethal temperature was 31.5°C) with some individuals surviving after 7 h. For statistical analysis the "survivors" are recorded as having survived 9 h; note that in any rank correlation analysis the actual value will not matter so long as it is greater than 7 h. For each clam we adjusted TTD for the temperature at which the experiment using that clam was done, by recoding TTD as deviation from the mean TTD in that experiment. However, all statistical analysis involving TTD as a variable produced the same results whether or not TTD was recoded in this way. For the following analysis and presentation of results we have therefore reverted to the use of simple TTD in hours; among-clam variation in tolerance to high temperature is sufficiently great that it swamps variation related to differences in experimental temperature over this (32−34.5°C) range. Electrophoretic analysis of tissues, and growth band analysis of shells, were done on the 178 clams from these three (32, 33, 34.5°C) experiments. Subsamples of tissue from 24 clams that were awaiting electrophoretic analysis were lost. Therefore, all statistical analyses of data derived from the 1980 material are based on 178 clams if a genetic parameter is not involved, and on 154 clams if it is. Bartlett's test of sphericity rejects ($P < 0.01$) the null hypothesis that all true correlations among the five variables (Table 1) are zero, and a similar result is obtained if the test is carried out on the Spearman rank correlation matrix. A principal component analysis on that correlation matrix is also presented (Table 1); following Marriott (1974) we consider only vectors associated with roots larger than unity. Principal component I may be interpreted as "increased heterozygosity and growth rate related to higher tidal level and greater age," bearing in mind that the growth rate index as calculated here is statistically independent of the variable "tidal level." (We have already demonstrated a strong relationship between growth rate and tidal level.) The relationship to greater age implies selection for heterozygotes, which thus represent increasing proportions of older age-classes. Principal component II may be interpreted as a relationship between higher growth rate and shorter TTD under high temperature stress.

The bivariate relationships and any tidal-level differences in those relationships were then examined, and the following were found to be statistically significant.

The overall ANCOVA model relating growth rate index, as a criterion variable, to degree of heterozygosity (the covariate), tidal level (the groups in the ANOVA part of the model), and interaction between heterozygosity and tidal level (difference in slopes between tidal levels), as predictor variables, is significant ($P < 0.01$) (Fig. 8). The slope of the growth-rate-versus-heterozygosity relationship differs between tidal levels ($P < 0.05$). A separate regression analysis for each tidal level indicates no relationship between growth rate and heterozygosity at the MLW level, and a

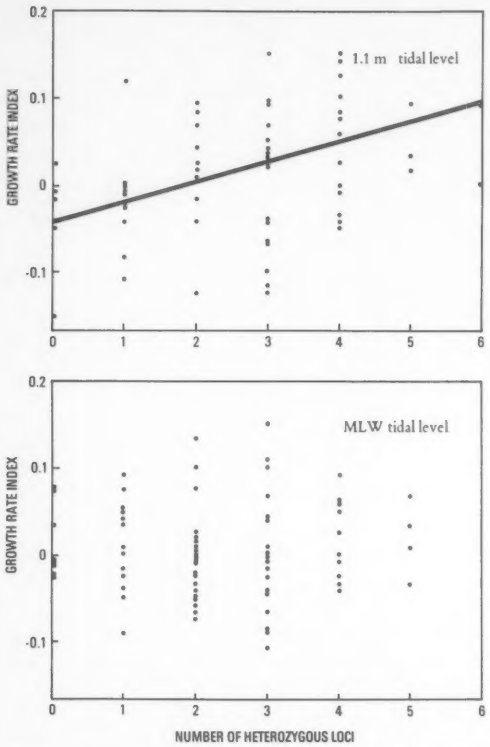

FIG. 8. The relationship between growth rate index (a measure of within-tidal level variation in growth rate among clams) and the number of heterozygous loci (out of six evaluated), shown separately for the two tidal levels. The growth rate index necessarily has a mean of zero at each tidal level. Only the 1.1-m tidal level relationship was statistically significant.

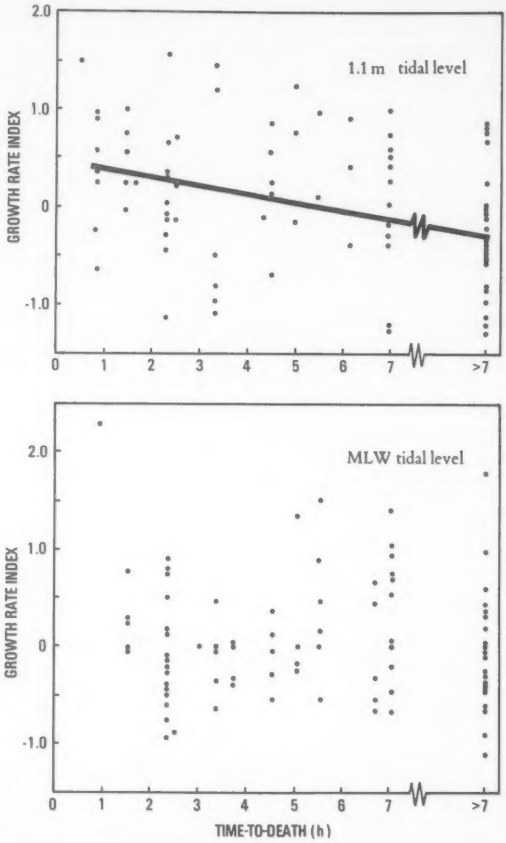

FIG. 9. The relationship between growth rate index (see Fig. 8) and time-to-death in the high lethal temperature experiment, shown separately for the two tidal levels. The experiment was of 7 h duration and therefore points at >7 h represent survivors. Only the 1.1-m tidal level relationship was statistically significant.

significant ($P < 0.01$) relationship, growth rate index = $-0.038 + 0.018$ (no. of loci heterozygous), at the 1.1-m tidal level. The Spearman rank correlation is also significant ($P < 0.01$) for the 1.1-m tidal level relationship. The RLINE procedure yields estimates of intercept and slope, respectively, of -0.045 and 0.022. The above Model I and RLINE estimates of slope are consistent with the expected downward bias in the Model I regression estimate of the slope (see discussion in Methods), caused by error in estimation of the predictor variable. The bias is a conservative one. In general the RLINE procedure yields slope and intercept estimates in similar agreement with Model I regression estimates; we will therefore not give RLINE estimates for each subsequent relationship.

The overall linear regression model relating growth rate index as a criterion variable, to TTD, tidal level, and the interaction between TTD and tidal level, as predictor variables, is significant ($P < 0.05$) (Fig. 9). The slope of the growth rate-versus-TTD relationship differs between tidal levels ($P < 0.05$). A separate regression analysis for each tidal level again indicates no relationship at the MLW level and a significant ($P < 0.01$) relationship, growth rate index = $0.043 - 0.0082$ (TTD), at the 1.1-m tidal level. The Spearman rank correlation is also significant ($P < 0.01$) for the 1.1-m tidal level relationship.

In both of the above relationships involving growth rate index as a criterion variable (Fig. 8 and 9), the significant relationship was only at the 1.1-m level. It is interesting that the variance in L_{t+1}, about each Walford Plot regression line, is greater at the 1.1-m than at the MLW level ($S_{1.1}{}^2/S_{MLW}{}^2 = 1.81$, $P < 0.01$). Therefore the coupling of growth rate with heterozygosity and with sensitivity to high temperature, at the 1.1-m but not at the MLW level, is associated with increased variability of growth rate at the 1.1-m level.

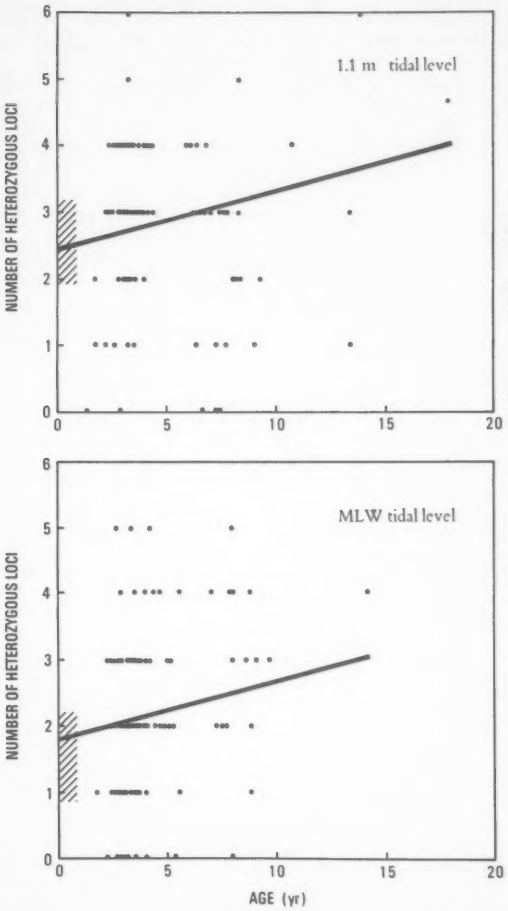

FIG. 10. The relationship between number of heterozygous loci (see Fig. 9) and age, shown separately for the two tidal levels. Slopes do not differ significantly between tidal levels, but intercepts do. The shaded bars on the ordinates represent 0.95 confidence limits on the intercepts of regressions calculated separately for each tidal level, with different slopes.

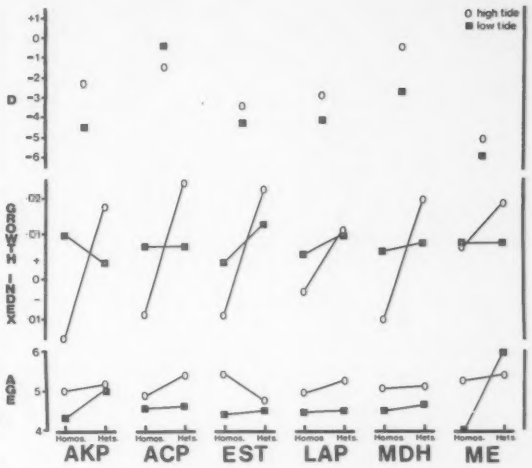

FIG. 11. *Top*: Mean heterozygote deficiency D at each locus, for each tidal level (high tide = 1.1 m level, low tide = MLW level). Negative D indicates an excess of homozygotes, compared with the prediction from the Hardy–Weinberg equilibrium. *Middle*: Mean growth rate index for homozygotes and heterozygotes, at each locus, by tidal level. *Bottom*: Mean age for homozygotes and heterozygotes, at each locus, by tidal level.

The overall linear regression model relating degree of heterozygosity as a criterion variable, to age, tidal level, and interaction between age and tidal level, as predictor variables, is significant ($P < 0.01$) (Fig. 10). The slope of the heterozygosity-versus-age relationship does not differ between tidal levels ($P > 0.05$), but intercepts do differ ($P < 0.05$) thus indicating a difference between tidal levels in degree of heterozygosity. Regressions with common slope were estimated for each tidal level: at the 1.1-m tidal level, heterozygosity = 2.34 + 0.0844 (age), and at the MLW level, heterozygosity = 1.88 + 0.0844 (age). The Spearman rank correlation is also significant ($P < 0.05$) for the pooled relationship. Such a heterozygosity-versus-age relationship suggests selection for heterozygotes relative to homozygotes throughout the lifespan of adults on the shore. A critical question is whether newly settled larvae (age zero) at each tidal level differ genetically; that is, does degree of heterozygosity begin at the same point for adult *M. balthica* at the two tidal levels? If not, then some kind of genetically based larval settlement behavior resulting in tidal level selection is implied. Our data (Fig. 10) leave this question open. Slopes do not differ significantly between tidal levels whereas intercepts do, implying different "beginning heterozygosities" and similar selection for heterozygotes thereafter. However, the probability level for the test of slopes was $\sim P = 0.2$, and there is obviously great scatter in the data. The 0.95 confidence limits on intercepts of the two tidal level regressions, based on separate slope estimates, show almost no overlap (vertical bars on the ordinates in Fig. 10). Thus the common slope model and the different slopes model both suggest different intercepts, but given the scatter in our data it can be no more than a suggestion.

LOCUS-SPECIFIC GENETIC RELATIONSHIPS

We have not pursued hypothesis-testing statistics to the individual locus level. Rather, we provide descriptive detail, which may not be real in all particulars, of previously validated relationships involving heterozygosity. Figure 11 shows locus-by-locus relationships involving heterozygote deficiency D, growth index, and age. The D statistic is calculated as the deviation of observed from expected (under the Hardy–Weinberg equilibrium) heterozygosity, divided by

the expected heterozygosity. Negative D indicates an excess of homozygotes, and a corresponding deficiency of heterozygotes. See Singh and Green (1983) for discussion. The *M. balthica* at Churchill are generally deficient in heterozygotes, and the lower is generally more deficient than is the higher tidal level population. The positive relationship between growth rate and heterozygosity at 1.1 m, and the lack of any relationship at MLW (Fig. 8), is also apparent at the locus-by-locus level. The general positive relationship at both tidal levels between degree of heterozygosity and age (Fig. 10), implying selection for heterozygotes, is also apparent at the locus-by-locus level.

Discussion

Macoma balthica at Churchill grow faster at the 1.1-m than at the MLW tidal level, and also differ genetically in a way (greater heterozygosity at a number of loci) that is consistent with a poorly understood but well-documented relationship between growth rate and heterozygosity. (This is an observational study and we cannot demonstrate causality; it is of course possible that the higher growth rate at 1.1 m is caused by higher temperature and has nothing to do with heterozygosity which could be caused by something else.) The same growth rate–heterozygosity relationship exists within the 1.1-m tidal level population but not within the MLW population. Sensitivity to high lethal temperature is associated with higher growth rate, but again only within the 1.1-m tidal level population. We do not claim to have imitated natural conditions in our high temperature experiments; this would be difficult to do given the ability of clams on the beach to escape from surface heat by burrowing. However, massive heat death mortalities of intertidal bivalve populations do occur, and at Churchill these heterozygosity–growth rate– heat sensitivity relationships appear to exist only at the tidal level more exposed to severe high temperatures. Although the Hudson Bay marine environment is considered to be arctic (Dunbar 1968; Hedgpeth 1957a), one of us (R.H.G.) was at Churchill during a week in July 1979 when daily highs were ~36°C. By chance, it was not at the time of lowest monthly or seasonal tides, nor were low tides around midafternoon. Young-of-year, reported by Lammens (1967) to remain near the substrate surface, are probably the most vulnerable stage.

The positive relationship between degree of heterozygosity and age suggests selection for heterozygotes, but the general deficiency of heterozygotes in the adult population suggests selection in the opposite direction — for homozygotes — during the period between meiosis and larval settlement on the shore. Singh and Green (1983) discuss this problem. Tracey et al. (1975) described heterozygote deficiency in intertidal *M. californianus*, with the deficiency greater in juveniles than in adults, as in this study. Subdivision of the reproductive population (the Wahlund effect) was suggested as the cause. No tidal level differences such as we have described here were found.

It is interesting that some relationships were not found here. Time-to-death under high temperature stress did not differ between tidal levels, despite the very different temperature regimes at those levels, and the demonstrated growth rate and genetic differences. Also there was no relationship between heat-sensitivity and age, at either tidal level. We cannot determine whether life expectancy differs between tidal levels because our collections cannot be assumed to contain a random sample of sizes, or of ages, from the natural population. We have avoided statistical analyses which require this assumption. Growth rates can be compared between tidal levels because they are derived from growth increments recorded by annual shell rings, rather than from sampled size or age distributions which might be biased estimates of the population age/size distributions.

Heterozygous adults appear to survive better, but individuals with higher growth rates, which tend to be more heterozygous at the 1.1-m tidal level, are at 1.1 m more vulnerable to high temperature than are slow-growers which tend to be more homozygous. This could be explained by infrequent heat-stress, which by chance has not occurred during the recent period over which the population sampled in 1980 has been alive. The population is a mixture of genetic types; it may be that at one extreme are individuals able to grow faster, survive better during most years, and reach high fecundity sizes sooner, but risk mortality if an improbable heat death event occurs. At the other extreme would be slower growing individuals that reach reproductive size later and in most years have poorer survival and contribute less to the population rate of increase, but that in the rare unpredictable year when the heat death event occurs, will have a better chance of surviving and contributing to reproduction.

Acknowledgments

We thank the Churchill Northern Studies Center for the use of their facilities. Comments by seminar audiences at the University of North Carolina, Juniata College, University of British Columbia, Université de Montréal, and National University of Singapore contributed to the final form of this paper. The Department of Geology of the University of Western Ontario assisted with shell sectioning, and R. Harris of the Department of Zoology with photography. We are grateful to the referees who made valuable suggestions. Special thanks are owed to the Department of Zoology of the National University of Singapore for providing the facilities for revision of the manuscript, and for some computer reanalysis of the data. This research was supported by an NSERC operating grant to R. H. Green.

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Solution to the "Char Problem" based on Arctic Char (*Salvelinus alpinus*) in Norway[1]

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NORDENG, H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. Can. J. Fish. Aquat. Sci. 40: 1372 – 1387.

Rearing and transplantation experiments demonstrate that three coexisting forms of Arctic char *Salvelinus alpinus* (anadromous, small and large freshwater residents) belong to the same gene pool. The parr of each form segregate into all three forms. Single individuals may manifest all three forms during their lifetime, successively attaining the appearance and spawning color of each form. Males mature at a younger age and smaller size than females. Hence, in char populations featuring two or more forms, males dominate in the early maturing form and females in the late maturing form. Char populations that feature only one form (sex ratio 1:1) seem to be established through natural selection for age at sexual maturity. Segregation during the young stage depends upon their genetic constitution and access to food. Offspring of the small resident parents produced more resident individuals and fewer smolts than did offspring of anadromous parents. An increased amount of food increases the resident fraction and reduces the fraction of anadromous char. It is demonstrated that the potential for anadromy exists in populations of char in the southern nonanadromous area, and that one reason for resident behavior in the smolt may be infection of the ureter fluke *Phyllodistomum conostomum* Olsson.

NORDENG, H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. Can. J. Fish. Aquat. Sci. 40: 1372 – 1387.

Des expériences d'élevage et de transplantation ont démontré que trois formes coexistantes de l'omble chevalier *Salvelinus alpinus* (anadrome, petit et gros dulçaquicoles non migrateurs) appartiennent au même effectif de gènes. Les tacons de chaque forme se transforment en l'une ou l'autre des trois formes. Un individu peut prendre les trois formes pendant son cycle vital, adoptant successivement l'apparence et la livrée de fraie de chaque forme. Les mâles atteignent la maturité à un âge et une taille inférieurs aux femelles. Ainsi, dans les populations d'omble qui possèdent deux formes ou plus, les mâles sont plus abondants chez la forme qui mature plus tôt et les femelles, chez la forme qui mature plus tard. La sélection naturelle par l'âge à la maturité sexuelle semble être le facteur déterminant des populations d'une seule forme (rapport des sexes 1:1). Chez les jeunes, la ségrégation dépend de leur constitution génétique et de l'accessibilité de la nourriture. La progéniture de petits parents non migrateurs comporte plus d'individus non migrateurs et moins de saumonneaux que la progéniture de parents anadromes. Une plus grande quantité de nourriture augmente la fraction d'ombles non migrateurs et réduit la fraction d'ombles anadromes. On démontre que le potentiel d'anadromie existe chez les populations d'ombles de la partie méridionale où les poissons ne sont pas anadromes et qu'une infection de l'uretère causée par le trématote *Phyllodistomum conostomum* Olsson peut expliquer la non-migration du saumoneau.

Received July 9, 1982
Accepted May 18, 1983

Reçu le 9 juillet 1982
Accepté le 18 mai 1983

THE "char problem" has long been an unsolved complex of questions concerning the systematics and ecology of Arctic char, *Salvelinus alpinus*. The problem arises from the phenomenon that Arctic char, throughout their circumpolar distribution, frequently occur in two or three coexisting forms of different size. In the southernmost areas of distribution all three forms are freshwater resident, and commonly designated dwarf, normal, and large (predatory) char (Haempel 1924; Neresheimer 1937; Fridriksson 1939; Reisinger 1953; Savvaitova 1969; Nilsson and Filipsson 1971; Dörfel 1974; reviewed in Johnson 1980). Corresponding forms in European river systems of anadromy may be characterized small resident, large resident, and anadromous char (Nordeng 1961; Gullestad 1975).

In principle, char forms differ in (1) age at sexual maturity, (2) sex ratio, (3) spawning color, (4) time and place of spawning, (5) feeding habits, (6) morphometric characters, and (7) migration. The variation in characters between sym-

[1]First presented at the International Symposium on Arctic charr, Winnipeg, May 1981.

Printed in Canada (J7000)
Imprimé au Canada (J7000)

patric forms is typically of the same kind throughout the entire range of distribution, and is often referred to as parallel development (Dörfel 1974) or homologous (parallel) inherited variation in characteristics (Savvaitova 1969).

Nilsson (1855), Reisinger (1953), and Brenner (1980) suggest that the coexisting forms may be regarded as phenotypes of genetically uniform populations, resulting from the influence of differences in environmental factors. However, most authors agree that the coexisting forms of Arctic char are reproductively isolated, although they disagree on the degree of relationship and allocation of taxa. Some consider the forms to be sibling species that were separated allopatrically in preglacial water bodies, and that subsequently invaded their present localities in postglacial times (Svärdson 1961; Nilsson and Filipsson 1971; Henricson and Nyman 1976; Klemetsen and Grotnes 1980). Behnke (1972, 1980) explains the coexisting forms by successive invasions, and considers some of them to be subspecies and even species. Frost (1963, 1965) and Savvaitova (1970, 1973, 1980) suggest that the forms may have developed sympatrically from a common ancestor; at the present time they have reached different stages of evolution and establishment.

In river systems along the Norwegian coast resident char occur together with Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, supplemented with anadromous char north of 65°N (Fig. 1). It is believed that char south of 65°N originated from anadromous ancestors and became nonanadromous during postglacial time. The explanation given is that during late postglacial time, summer temperatures in the Gulf Stream, south of 65°N, gradually became too high for the char. The char thus became marine relicts in their river systems (Huitfeldt-Kaas 1918; Ekman 1922). However, recent continuous measurements (Sætre and Ljöen 1972) indicate that temperatures in coastal waters both south and north of 65°N are 4−11°C during the summer period of sea migration of brown trout and char. The reason for resident behavior during postglacial time may then be due rather to changes in freshwater environmental factors or genetic constitution in the char themselves, than in temperature effects.

In Øvervatn[2], Salangen river system, north Norway (Fig. 1), small resident, large resident, and anadromous char coexist (Nordeng 1961). The three forms generally spawn at separate areas indicating that they may be reproductively isolated (Table 1). On the other hand, young char in the lake exhibit a single phenotype (Nordeng 1961), with a sex ratio of 1:1. Although the sex ratio in the three forms is different, the overall ratio approximates 1:1 as in young char. This indicates that the three forms may belong to the same gene pool (population). To decide whether the three forms in Øvervatn are reproductively isolated or belong to the same population, I studied their progeny in rearing and transplantation experiments. In parallel experiments I studied progeny of Arctic char from south Norway, to decide whether resident behavior results from environmental factors or genetic constitution. The parental stocks were from Bergen and Voss, south Norway (Fig. 1); they resemble the northern anadromous char both in appearance, and age and size at sexual maturity.

[2]The suffix "vatn" means lake.

Environment and Fish Community

Salangen, North Norway

The Salangen river system, situated within the area of anadromy of Arctic char (Fig. 1), is one of the few river systems in Norway in which salmonid species have remained genetically unaffected by human manipulation. Like most river systems in north Norway, the Salangen supports anadromous and resident individuals of Atlantic salmon, brown trout, and Arctic char. The resident salmon consist exclusively of precocious parr males, whereas resident trout and char also include females. Resident char fall into two forms, small and large. In anadromous char and trout the life history and pattern of migration are practically identical (Fig. 2). Each yearly migratory cycle ends with the participating categories (mature and immature veteran migrants and smolts of the year) returning to their freshwater habitats. In salmon, on the other hand, smolts and maturing salmon at sea exchange habitat during the migration period. Atlantic salmon and brown trout spawn in riffles throughout the river system. The various char forms spawn both in the river and in the lake (Øvervatn). Tagging experiments (unpublished) indicate that lake and river anadromous char may be reproductively isolated.

The three forms of Arctic char in Øvervatn exhibit the same kind of variation in characters (Table 1) as in coexisting forms throughout the distribution area (Savvaitova 1969).

Sexual Maturity and Sex Ratio

Among young char (parr) there is only one phenotype (Nordeng 1961), and the sex ratio is 1:1. During a period of 7 yr (the young stage), parr segregate into sexually mature individuals (natural resident males and females) and smolts [Fig. 2(I)]. Sexual maturation is initiated at an age of 2 yr and smoltification at 3 yr. The first to reach sexual maturity are males. During sexual maturation in the subsequent years, mature males exceed females in number, but the proportion declines from year to year. Small resident char maturing at an age of 2−6 yr thus exhibit more males than the large resident char maturing at an age of 3−7 yr; both forms show males in excess (cf. Table 1). Consequently, individuals that do not mature during the young stage, but smoltify and become anadromous char, show an excess of females. Anadromous char attain sexual maturity at an age of 4−8 yr, after their first, second, or third migratory cycle in the sea.

Spawning Areas

In Øvervatn, the spawning areas of anadromous char, large resident, and small resident char are situated close to each other on the northern side of the lake, and will here be called areas I, II, and III, categorized subjectively. Area I (Flåglandet), which is considered the most favorable, is situated at a depth of 2−6 m with a substratum of pebbles and gravel. Area II (Løehola) lies at the same depth, but the substratum consists of pebbles and gravel mixed with a little mud. Area III (Ressestolan), situated between area I and II, must be regarded as the least favorable spawning area as the substratum is composed of rocks and a little sand, with very

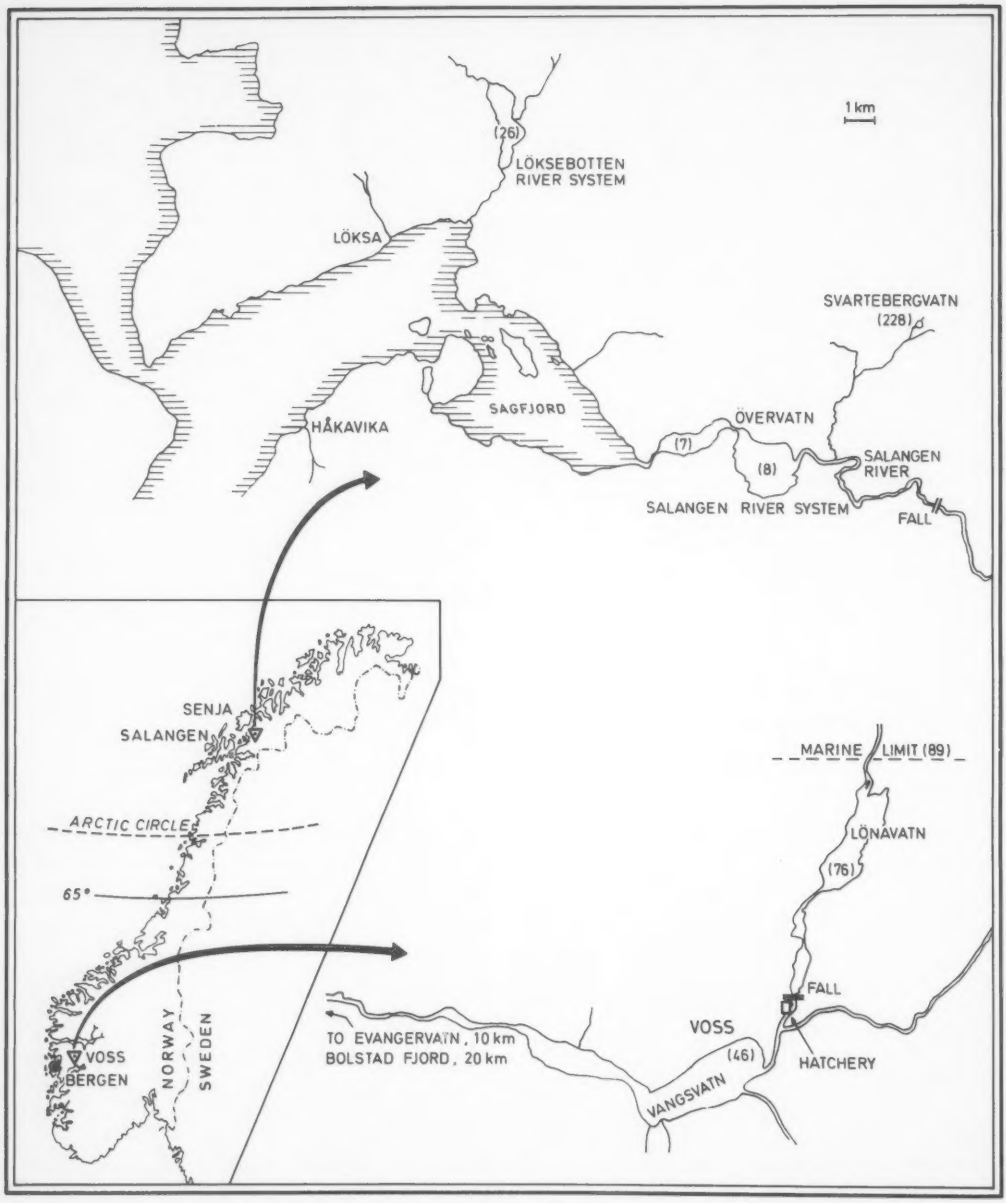

FIG. 1. The study area in south and north Norway and the hatchery below Rognsfossen waterfall at Voss. Number in parentheses = height (m) above sea level.

steep gradients down to 30 m. There seems to be competition for the spawning areas. Anadromous char spawn mainly in area I, large resident char mainly in area II, and small resident char exclusively in area III. Anadromous char and large resi-

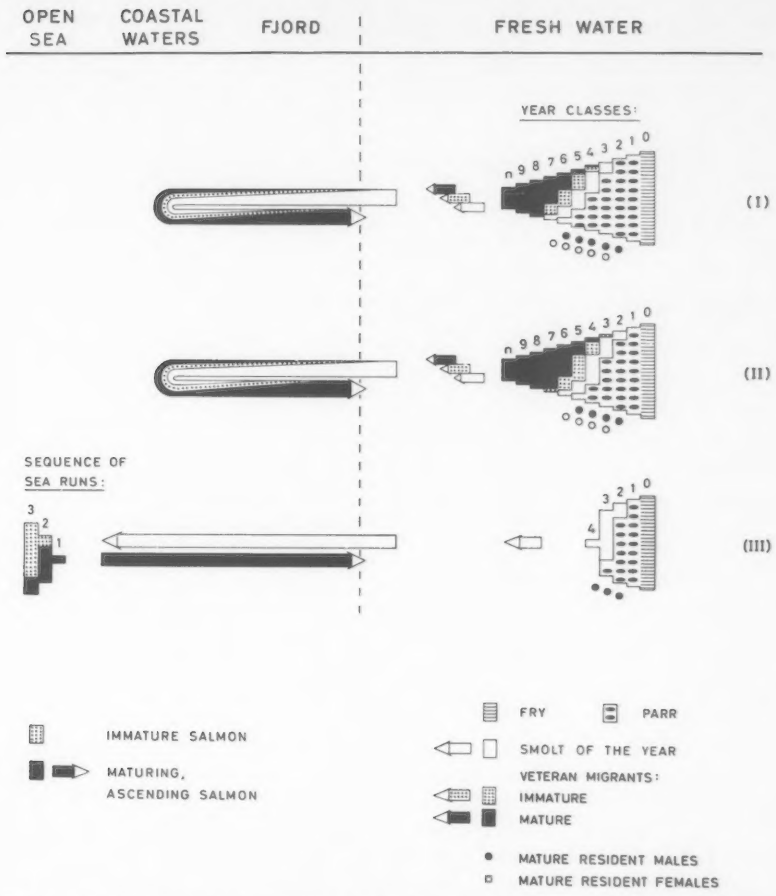

FIG. 2. Life history and migratory pattern in Arctic char *Salvelinus alpinus* (I), brown trout *Salmo trutta* (II), and Atlantic salmon *Salmo salar* (III), Salangen river system, north Norway. The figure is based on the char material in Nordeng (1961) and unpublished data on trout and salmon. The timing of the seasonal migrations is given in Nordeng (1977).

dent char keep their respective areas for themselves, whereas small resident char must share theirs with pairs from both neighboring groups.

FEEDING HABITS

Between annual spawnings resident char feed in freshwater, whereas anadromous char acquire the main part of their food during their stay in coastal waters. After homeward migration, anadromous char also take some food while schooling along the bottom or in the pelagic zone of the lake. Large resident char exhibit both schooling and benthic behavior, whereas small resident char feed on the bottom along the shores and in the inlets and outlets of the lake.

Resident char may change form and feeding habit. According to well-definable spawning zones in otoliths some resident char transform into anadromous char after spawning 1–3 times (Nordeng 1961). This applies to both sexes and accounts for about 9% of anadromous char. After transformation, these previously resident char grow and behave like anadromous char and remature after their second or third period in the sea.

GROWTH RATE AND TOTAL SIZE

Differences in growth rate and total size are often regarded as particularly characteristic of coexisting forms of Arctic char. Extensive annual growth during the immature stage, in the three forms of Salangen char, shows in the otoliths as wide, opaque, summer zones; stagnant growth at the mature

TABLE 1. Life history characteristics of Arctic char *Salvelinus alpinus* in Øvervatn, Salangen river system, north Norway, based on material in Nordeng (1961).

Characteristics	Small resident char	Large resident char	Anadromous char
Age (year)	2–13	3–15	4–14
Length (cm)	14–22	21–38	26–56
Weight (g)	25–90	70–460	160–1650
Sex ratio M:F	4:1	2:1	1:3
Spawning color	Pale grey	Yellow, red	Golden red, red
Spawning season	Autumn	Autumn	Autumn
Spawning frequency	Annual	Annual	Annual
Max. no. of spawning	10	13	7
Spawning areas I, II, III	III	II (III)	I (III)
Feeding habit	Benthic	Benthic–pelagic	Benthic, pelagic
Age at sexual maturity (yr)	2–6	3–7	4–8
Length at sexual maturity (cm)	14–22	21–27	26–48
Average length at sexual maturity (cm)	17.2	26.7	35.8
Average growth rate in mature stage (cm)	0.2	0.3	2.6

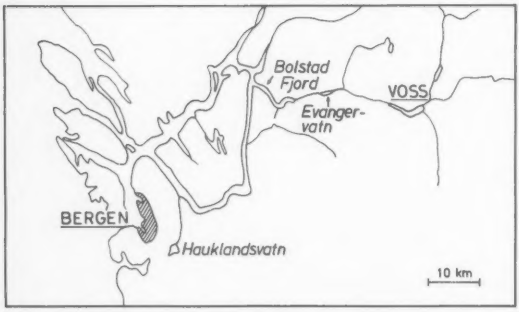

FIG. 3. Study area in south Norway.

stage is manifested as narrow, hyaline, spawning zones, or dense edges in corresponding scales (Nordeng 1961). Annual growth rate during parr stage is similar in all three forms. Growth rate in the mature stage depends on the size of the fish at sexual maturity. This implies different growth rates in the three forms and divergent growth during the mature stage (see Table 1).

BERGEN AND VOSS, SOUTH NORWAY

As in northern Norway, the coastal river systems in south Norway support Atlantic salmon, anadromous brown trout, and resident individuals of each species. Resident char are commonly present in the lakes of the river system, but seagoing char are absent.

During a pilot investigation in south Norway, while searching for suitable populations for our rearing and transplantation experiments, I found small and large resident char corresponding to the natural residents in the Salangen river system, north Norway. These forms were found above impassable waterfalls, together with resident brown trout, and below waterfalls in company with resident and anadromous brown trout and Atlantic salmon. However, in two river systems I found a third form which resembles anadromous char in most characteristics. The localities were Hauklandsvatn, near Bergen, and the Voss river system, both of which drain into the same system of fjords (Fig. 3).

In Hauklandsvatn, situated above a waterfall, 46 m above sea level, small and large resident char were found in addition to the third form which resembles anadromous char in appearance, size of the immature (26–35 cm) and mature (30–42 cm) stages, growth pattern, and age at sexual maturity. The scales of these char showed typical river–sea growth, despite the fact that they had spent their life exclusively in the lake. The change in the growth pattern of the scales occurs at an age of 2, 3, or 4 yr at a body length between 15 and 21 cm. The yearly length increment in the immature "post-smolt" stage was 8–16 cm, at least as high as that of the anadromous char of the Salangen river system (6–11 cm). This form is designated "potential anadromous char," because in all characteristics, except migration, it corresponds to anadromous char. The freshwater resident brown trout in Hauklandsvatn, which use the inlet brooks during parr stage, also showed a marked growth change in their scales.

The Voss river system supports Atlantic salmon, anadromous brown trout, and resident individuals of both species. Potential anadromous char were found both in Vangsvatn below the waterfall (Rognsfossen, 16 m) and in the ~8000-yr-old Lønavatn, situated above the fall, near the limit of former marine inundation (Fig. 1). In Lønavatn I expected to find the early maturing, small and large, resident char typical for such localities. However, I only found the potential anadromous form coexisting with resident brown trout and threespine sticklebacks *Gasterosteus aculeatus*, all obviously originating from anadromous ancestors. In Vangsvatn, the potential anadromous char were found together with small and large resident char. The potential anadromous char in the two lakes differ in body form, being slender in Vangsvatn but having a deep body in Lønavatn. In Lønavatn, char spawn in a restricted area of mediocre quality

TABLE 2. History of Arctic char *Salvelinus alpinus* hatched 1960–71 and used in rearing and transplantation experiments. The parents were small resident (SR), large resident (LR), and anadromous char (A), north Norway, and potential anadromous char (A*), south Norway. The offspring were reared at Voss and studied in the hatchery; some were released in different localities in north and south Norway.

Parents		Locality	Feeding intensity	Number of offspring at 1+	Number released			
					North Norway		South Norway	
					Salangen	Senja	Voss	Bolstadfjord
			North Norway					
Salangen river system								
1960	SR	Lake	Low	2705			587	72
	LR	"	Low	1629			299	26
	A	"	Low	4046			615	35
1965	A	"	Moderate	1817	519		174	
1970	A_2 of A 1965	Hatchery	"	687				
	SR	Lake	"	3361	1734			
	A	River	"	381		215[a]		
1971	A	River	High	1640	429	85		
			South Norway					
Bergen								
1970	A*	Hauklandsvatn	Moderate	842		442[a]		
Voss river system								
1970	A*	Vangsvatn	Moderate	1000				
	A*	Lønavatn	Moderate	517		306[a]		
1971	A*	Lønavatn	High	3091		356		210
Total				21716	2682	1404	1675	343

[a]Released through a hole in the ice cover of the lake. None were recaptured.

in the middle of the lake (cf. Matzow et al. 1976; Jonsson and Østli 1979).

Resident behavior in the southern potential anadromous char may be congenital or it may be due to environmental factors. The only relevant environmental factor I found was the trematode *Phyllodistomum conostomum* Olsson which infects the ureters of char. This fluke was found regularly in southern char down to a length of 17 cm, except for char in Hauklandsvatn. The ureters could be infested with more than a dozen flukes each. Flukes seem to occlude the ureters and damage the epithelium. In time, the ureters become white and elongated, forming zigzag bands which may be calcified. Infected char are sluggish and do not attempt to leave their lakes either against or with the current.

Among the potential anadromous char of Hauklandsvatn (Bergen), Vangsvatn, and Lønavatn (Voss), char in Lønavatn exhibit the longest span of residency, ~8000 yr. I considered the potential anadromous Løna char and the anadromous Salangen char as particularly useful for comparative rearing and transplantation experiments on resident and anadromous behavior. Therefore, we built a hatchery with a water supply from Lønavatn (Fig. 1). In this way offspring from Løna char would be reared under their natural conditions whereas offspring from Salangen char would be exposed to the environment in which Løna char had been resident for ~8000 yr.

Materials and Methods

Our hatchery at Voss is furnished with 11 troughs measuring 3 × 1 m. To prevent infection of the ureter fluke *Phyllodistomum conostomum*, the water supply was filtered through plankton nets of mesh size 0.5 mm.

In the rearing and transplantation experiments the parents were small resident, large resident, and anadromous char from the Salangen river system, and potential anadromous char from Bergen and Voss. The offspring of each group originated from two to four males and several females. History of the material is given in Table 2. By personal judgment the feeding intensity during the rearing experiments was successively increased (low, moderate, high). In 1960, at low intensity, the offspring were fed by hand four times a day; food was a worm-shaped mixture composed mainly of beef liver and heart. In subsequent experiments the offspring were supplied with pellets 40 times a day (07:00–20:00) from an automatic feeding apparatus. Moderate feeding (1965, 1970) refers to half capacity of the feeding apparatus, and high intensity (1971) to full capacity, resulting in an excess of food in each trough.

During the first autumn, at an age of 0+, char in each trough were counted and a sample was sexed and measured. At this age the number of fry in each trough was around 2000. Owing to natural death and losses during cleaning, numbers decreased to 900–1100 at an age of 1+ when the examination of the fish started. At the end of each growth period in November–December the parr of the year in each trough were counted, measured, and classified. According to their appearance and coloration the immature individuals were

classified into parr and presmolt. The mature individuals were classified into small resident (10.5–21.9 cm) and large resident char (22.0–28.0 cm). The mature char were removed, whereas the presmolts were marked by finclipping and then returned to their respective troughs. During the classification period a few parr escaped and some were killed for sampling of scales, otoliths, and examination of the ureters for the presence of the fluke *P. conostomum*. These unclassified individuals, less than 6% of each form, were omitted from the data analysis. Subsequent examination of the ureters of several thousand char not used in the transplantation experiments revealed that none were infested with the ureter fluke, even after 6 yr in the hatchery.

The offspring used in the transplantation experiments consisted of individuals classified as mature small and large resident char, parr, and smolt. The char were tagged in the hatchery and released at an age of 1+ and 2+ in late autumn or in early spring, just before downstream migration of natural anadromous salmonids. In the Voss river system the char were released in the upper part (Vangsvatn), the lower part (Evangervatn), and the Bolstad fjord outside. Char transplanted to north Norway were transported by air. Offspring of Salangen chars were released in Øvervatn, in their parental river system. At the Isle of Senja, offspring of both anadromous and potential anadromous char were released in Vardnesvatn, situated upstream of a fish trap described by Mathiesen and Berg (1968). Maximum summer temperature in the Voss, Salangen, and Vardnes river systems is about 19, 15, and 19°C, respectively.

Transplanted char were captured by local fishermen and ourselves over a period of 5 yr. Tag returns were accompanied by scales and information on place and time of recapture, total length of fish, and sex. Based on this information and the scale characteristics (Nordeng 1961), I classified the recaptured char as parr, small resident, large resident, and anadromous char. In the Salangen experiment char captured in freshwater before the end of the first natural downstream migration (July 20) were not classified.

In addition to the material presented in Table 3, 150 char from Svartebergvatn were collected in 1981. This lake drains via waterfalls into the Salangen river (Fig. 1), and is populated with landlocked small resident char. They are descendants from the fry of anadromous char released in 1920 by local fishermen. The parents originated from spawning area I in Øvervatn (cf. Table 1).

Results

The Rearing Experiments

The aim of the first rearing experiment (1960) was to reveal the relationship between the three forms of Arctic char in Øvervatn (Salangen river system, north Norway). Offspring of small resident, large resident, and anadromous parents were studied during their whole lifetime in the hatchery at Voss, south Norway.

During the rearing period, development in the three groups of offsprings was in principle identical. The sex ratio was 1:1 as in the natural young char. Each offspring segregated into smolts and mature individuals, the latter classified as small and large resident char (Table 3). The successive segregation of parr during the young stage (age 0+ to 4+) is given as total number in Table 4, and as percentage in Fig. 4.

TABLE 3. The total segregation in percent in reared offspring of small resident char (SR), large resident char (LR), and anadromous char (A) *Salvelinus alpinus* during the young stage. The parents were from Øvervatn (Salangen river system, north Norway), and the offspring were reared at Voss (south Norway).

		Offspring		
Parents	Number	SR	LR	A
SR×SR	2705	67.9	10.8	21.3
LR×LR	1629	66.9	11.5	21.6
A×A	4046	62.9	14.2	22.9

Age 0+ — The newly hatched alevins measured 16–18 mm. At a body length of about 10 cm, young char lost their irregular finger or parr marks, and became silvery. Already in June a pronounced group of large individuals developed in each trough and reached a body length of 10–15 cm by the end of the growth period in November–December. At this time faint finger marks reappeared and were present for a few months. None of the young char matured, and all were classified as parr.

Age 1+ — During this growth period the largest parr in each trough developed in two directions, sexual maturation or smoltification. The parr that reached sexual maturity lost their silvery coloring and attained a pale spawning dress. Except for a total of 15 females (0.5%) the maturing individuals were males, measuring 10–22 cm at the end of the growth period. Length interval and spawning dress corresponded to small resident char in the parental river system, and they were classified as such. The nonmaturing large parr retained their silvery dress at the end of the growth period, and exceeded the maturing char in growth. These char were classified as presmolt.

Age 2+ — The largest of the remaining parr from the previous year segregated into (1) presmolts, (2) mature females, and (3) some mature males. The body length of the mature individuals at this season (12–28 cm) had a normal distribution (Fig. 4) and corresponded to the total length interval of the natural small and large resident char at sexual maturity (cf. Table 1). Spawning color of the hatchery char was not very pronounced and could not be used as a definite criterion for classification into small and large resident char. These mature char were therefore artificially divided according to the length interval found in nature, into small resident char (21.9 cm and smaller) and large resident char (22.0 cm and larger).

Age 3+ — As in the previous year the largest parr segregated into presmolts, mature females, and a few males. In this

FIG. 4. The successive segregation (percent) in reared offspring of small resident (SR), large resident (LR), and anadromous char (A) *Salvelinus alpinus* during the young stage. The parents were from Øvervatn (Salangen river system, north Norway) and the offspring reared at Voss, south Norway. The figure includes the offspring in two troughs of each type.

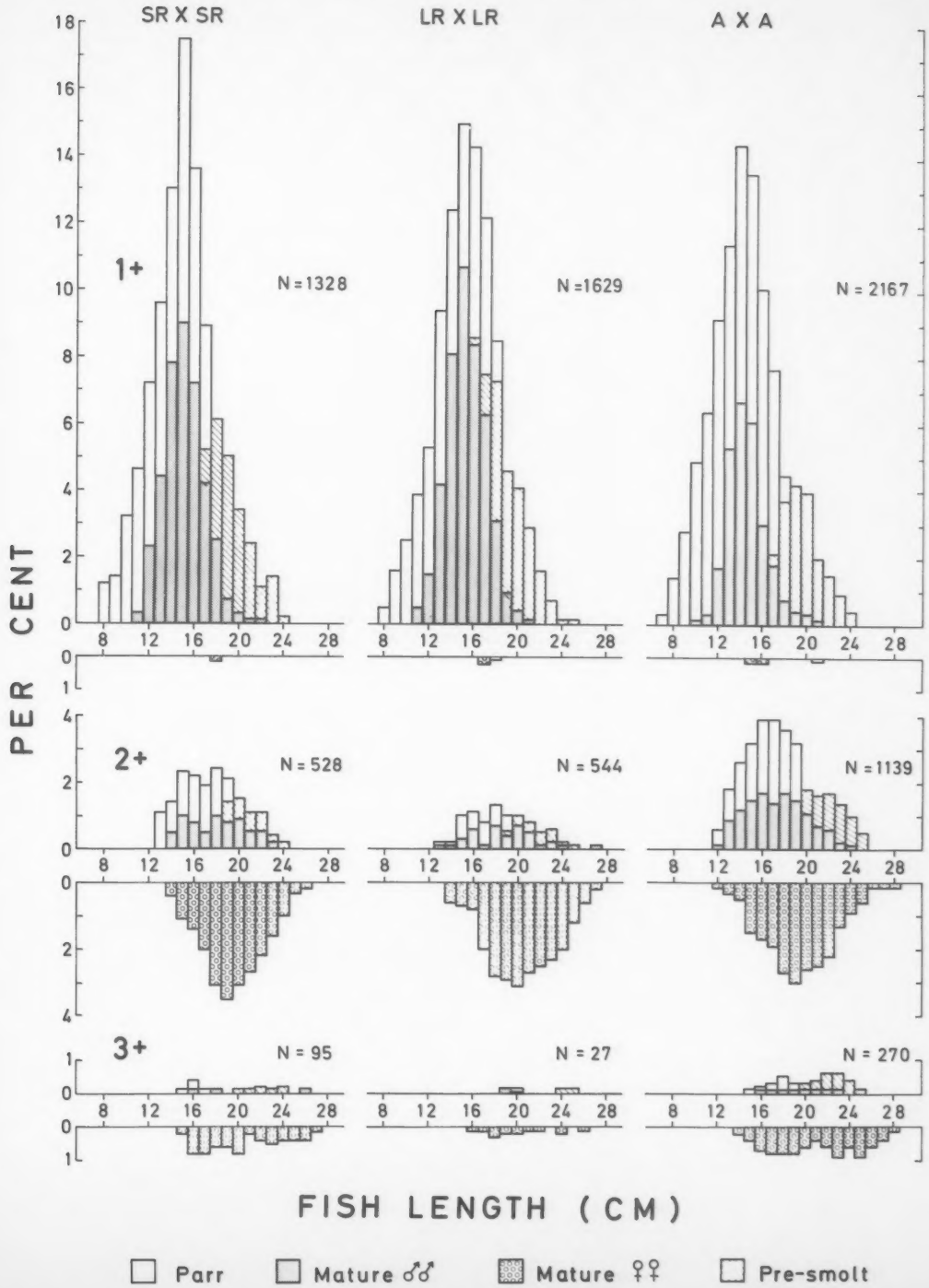
SR X SR
LR X LR
A X A
1+
2+
3+
N = 1328
N = 1629
N = 2167
N = 528
N = 544
N = 1139
N = 95
N = 27
N = 270
PER CENT
FISH LENGTH (CM)
Parr
Mature ♂♂
Mature ♀♀
Pre-smolt

TABLE 4. The successive segregation in total number in reared offspring of small resident char (SR), large resident char (LR), and anadromous char (A) *Salvelinus alpinus* during the young stage. The parents were from Øvervatn (Salangen river system, north Norway), and the offspring were reared at Voss (south Norway). P = parents, F_1 = offspring, M = male, F = female.

	P:	SR × SR				LR × LR				A × A			
Age	F_1:	SR	LR	A	Sum	SR	LR	A	Sum	SR	LR	A	Sum
1+	M	1020	4	472	1502	762	1	318	1085	1239	2	604	1850
	F	6	0			4	0			5	0		
2+	M	210	25	84	989	57	11	29	517	436	60	226	1637
	F	474	196			251	169			651	264		
3+	M	5	2	16	208	2	0	4	27	12	9	76	535
	F	122	63			14	7			202	236		
4+	M	0	1	3	6	—	—	—	—	1	0	19	24
	F	1	1							1	3		
SUM	M	1235	32	575	2705	821	12	351	1629	1688	71	925	4046
	F	603	260			269	176			859	503		

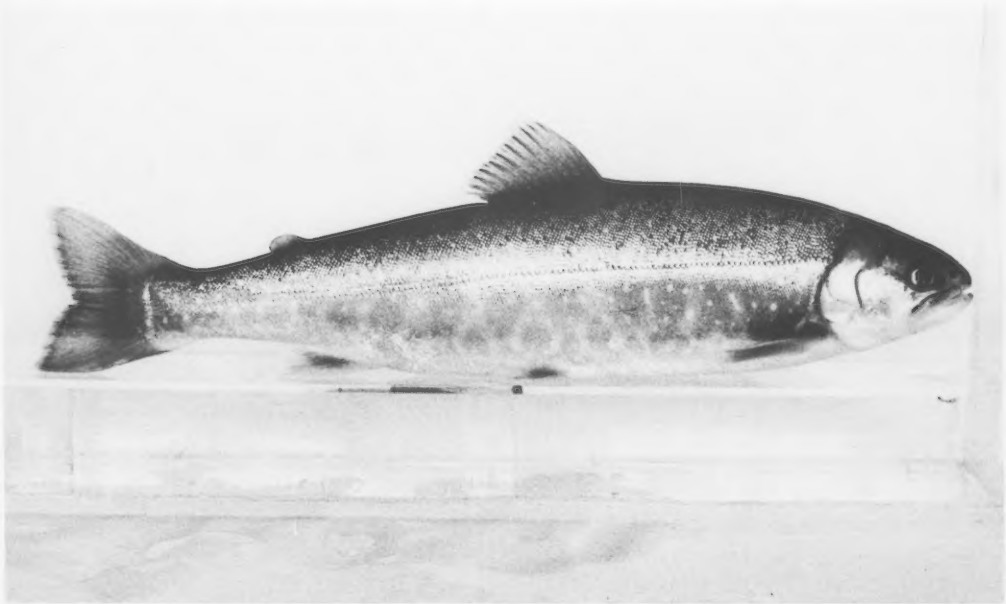

FIG. 5. Immature anadromous char *Salvelinus alpinus*, 35.0 cm, and 3 yr old. The char smoltified at an age of 2 yr (2+) and 22 cm, and is offspring of small resident char from Øvervatn (Salangen river system, north Norway).

season segregation in the offspring of large resident char concluded; i.e. all parr had either become sexually mature resident char or smolt.

Age 4+ — The few remaining parr from the previous year, the offspring of small resident char, and anadromous char segregated into presmolts, mature females, and males, thus concluding the young stage in these offspring (cf. Table 4).

In each type of offspring the males reached sexual maturity at a younger age and smaller length than did females (Fig. 4). This resulted in a dominance of males in the length interval occupied by small resident char, whereas females dominated in the length interval occupied by large resident char.

At the immature stage (Fig. 5) individuals classified as presmolts achieved a yearly length increment of 10 cm or more, corresponding to the natural anadromous char. They reached sexual maturity at an age of 3+ to 6+ with a body length of 26–59 cm.

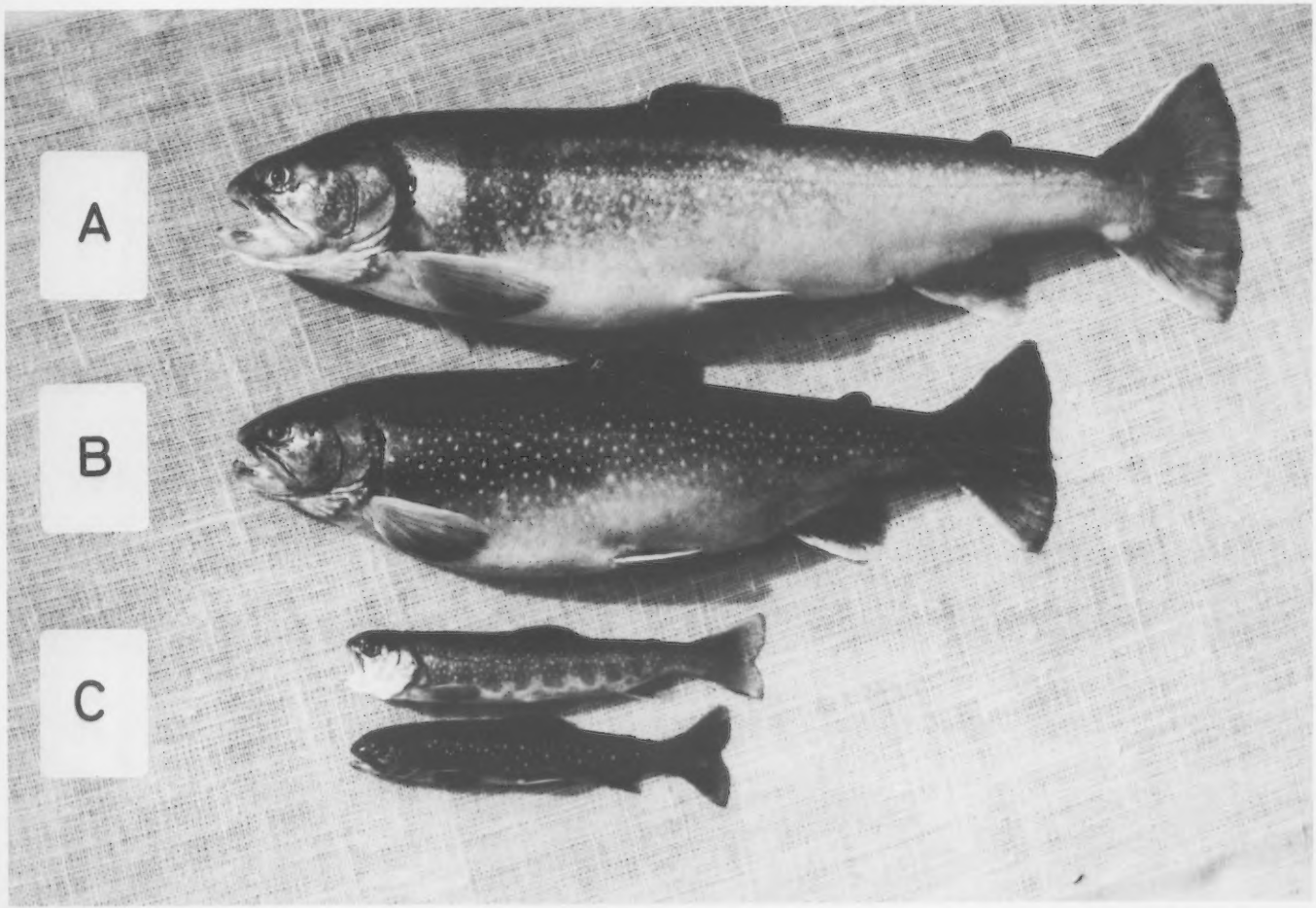

FIG. 6. Individuals of the same brood of small resident char *Salvelinus alpinus* from Øvervatn (Salangen river system, north Norway). The char were reared for 6 yr at Voss, south Norway. (A) Anadromous char, female, 56.5 cm. The char smoltified at an age of 1 yr (1+) and 25.2 cm, and matured at 4+ and 51.5 cm. (B) Large resident char, female, 44.9 cm, which matured at an age of 2 yr (2+) and 27.8 cm. (C) Small resident char, 20–21 cm, matured at an age of 1 yr (1+) and 17.5 cm.

TABLE 5. Segregation in young char *Salvelinus alpinus* originating from small resident (SR) and anadromous (A) parents, Salangen river system, north Norway. The char were reared at Voss, south Norway, and released into their parental river system in spring and autumn 1967, 1971, and 1972. The recaptured char were classified as parr, small resident (SR), large resident (LR), and anadromous (A).

Parents	Released	Recaptured	Classified in %				Not classified, %
			Parr	SR	LR	A	
SR	770	219 (28.4%)	16.9	8.2	11.9	42.9	20.1
A	537	154 (28.7%)	7.8	5.2	13.6	63.6	9.8

In the offspring of each group sexual maturity was initiated at age 1+ in small resident, 2+ in large resident, and 3+ in anadromous char, that is, 1 yr earlier than in the corresponding forms of the parental river system (cf. Table 1). As a whole, maturation extended over a period of 6 yr; from age 1+ in small resident char to age 6+ by the time maturation in anadromous char was completed. The individuals from the same cohort may, thus, reach sexual maturity at body lengths extending from 10 to 59 cm, demonstrating the well-known plasticity in Arctic char (Fig. 6).

The rearing experiment demonstrates that each form of the Salangen char reproduces itself and the other two forms. Thus, the three forms belong to the same population as indicated in the investigation on natural char in the Salangen river system (Nordeng 1961, fig. 19). In the three types of offspring the segregation was significantly different ($\chi^2_4 = 25.69$, $P < 0.01$), depending upon parental form (Table 3).

Development in the offspring of potential anadromous char originating from Hauklandsvatn (Bergen), Vangsvatn, and Lønavatn (Voss river system) was in principle similar to that described for Salangen char. Sex ratio in young char was 1:1. During the young stage each group segregated into individuals which were classified as resident char or smolts, though in different proportions depending upon ancestry (cf. Fig. 7).

Early maturing small resident and late maturing anadromous Salangen char represent the extremes of age at sexual maturity within their gene pool. Offspring of small resident parents produced more resident individuals and fewer smolt than offspring of anadromous parents. This difference (Table 4) was already significant at an age of 1+ ($\chi^2_1 = 34.0$, $P < 0.001$), indicating that the age at sexual maturity of the parents influenced the age at sexual maturity of their offspring.

Transplantation Experiments

Char used in the transplantation experiments were reared at Voss under conditions which prevented infection by the ureter fluke *P. conostomum*.

RELEASE IN THE SALANGEN RIVER SYSTEM

Char released originated from small resident and anadromous char from Øvervatn (Salangen river system) and anadromous char from the Salangen river. The aim of the experiment was to verify the segregation in young char (parr) observed in the hatchery, test the behavior in individuals classified as small and large resident char, and test the capacity for anadromy after rearing in the nonanadromous area at Voss.

Irrespective of parental type (small resident and anadromous) young char (16–23 cm) segregated into small resident, large resident, and anadromous char (Table 5), just as in the hatchery. Offspring of anadromous char produced more smolts than offspring of small resident char. However, the difference is not significant ($\chi^2_2 = 4.01$, $P > 0.05$).

Irrespective of parental type (small resident and anadromous), char classified as small resident and large resident did not migrate to the sea (Table 6) apart from some that transformed into anadromous char after a period as residents. Some of the large resident char transformed into anadromous char, and some small resident transformed into large resident and into anadromous char. Resident char originating from anadromous parents transformed into anadromous char in a significantly higher proportion than in offspring originating from small resident char ($\chi^2_2 = 15.76$, $P < 0.001$). The patterns of transformation described above indicate that single individuals may manifest themselves in all three forms during their lifetime. This is supported by the development seen in the offspring of small resident char (Table 6). In the hatchery all (851 + 114) were classified as small resident char at an age of 1+. When released (2+) 114 had transformed into large resident char. Of these, seven (6.1%) were recaptured as anadromous char (3+).

Further, a control group of 81 young char originating from small resident and anadromous char held in the hatchery segregated and transformed in a manner similar to that of the transplanted char. At an age of 2+ there was a loss of 7, whereas the rest segregated into smolts (17), small resident (15), and large resident char (42). The following year, three of the large resident char transformed into anadromous char. Of the 15 small resident char, 10 became large resident and 3 became anadromous char.

The result of the Salangen transplantation experiment confirmed the rearing results. Young char (parr) segregated into small resident, large resident, and anadromous char (Table 5). Further, the char classified as small and large resident behaved according to their classification, except for some that transformed from one form into another. The transplantation experiment also proved that the anadromous quality in the Salangen char had not been affected by day length or by abiotic factors in the hatchery water when reared in the nonanadromous area at Voss. The anadromous char (Tables 5 and 6) accompanied the natural anadromous char on their seasonal migrations to the sea, and none were recaptured in other river systems.

TABLE 6. Transformation in mature char *Salvelinus alpinus* originating from small resident (SR) and anadromous (A) parents, Salangen river system, north Norway. The char were reared at Voss, south Norway, classified as small resident (SR) and large resident char (LR), and released into their parental river system in spring and autumn 1967 and 1972.

Parents	Offspring	Released	Recaptured	Classified in %			Not classified, %
				SR	LR	A	
SR	SR	851	146 (17.2%)	40.4	24.7	21.9	13.0
	LR	114	24 (21.1%)		70.8	29.2	
A	SR	338	45 (13.3%)	26.7	20.0	46.7	6.6
	LR	72	19 (26.4%)		31.6	57.9	10.5

RELEASE IN VARDNESVATN, SENJA

To test their capacity for anadromy, offspring of potential anadromous char were released in a northern river system containing anadromous char.

Offspring of the potential anadromous char from Lønavatn were released into Vardnesvatn (Senja), accompanied by offspring of anadromous char from the Salangen river as a control. The char originated from the 1971 brood and were released in autumn, 1973, and in early spring, 1974. They were immature and 18–32 cm long, which corresponds to anadromous char in the smolt and postsmolt stage. Downstream migration was monitored by a fish trap situated in the outlet river. During June and July the char accompanied the natural anadromous char on their migration to the sea.

Of the 85 char in the control group, 72 (84.7%) were recorded in the trap. Of the 356 potential anadromous char, 51 (14.3%) were recorded and two were recaptured in other river systems without prior recording in the trap. In contrast to the control group of Salangen anadromous char, the site of the tags in most of the Løna char was infected with *Saprolegnia* sp. After completion of the downstream migration Vardnesvatn was surveyed with gill nets to determine whether Løna char had remained in the lake. Only nine Løna char were recaptured. They were in very poor condition and heavily infected with *Saprolegnia*. This indicates high mortality in the introduced Løna char. Those registered in the trap may thus represent surviving char migrating to the sea.

Of the char registered in the trap only three Salangen and two Løna char returned to the Vardnes river system. Two Salangen char were recaptured in the sea, and six in other river systems.

In spite of high mortality in Løna char, this experiment indicates that the capacity for anadromy exists in southern potential anadromous char.

RELEASE IN THE VOSS RIVER SYSTEM

The aim of this experiment was to test the capacity for anadromy in offspring of Salangen char when released in a southern river system, where natural char are resident and infected with *P. conostomum*.

Offspring of all three Salangen char, classified as smolts (1433) and resident char (242), were released into Vangsvatn and Evangervatn in late autumn (age 1+) and early spring (age 2+), just before commencement of the downstream run of natural brown trout and Atlantic salmon smolts.

TABLE 7. Recaptures of Løna char *Salvelinus alpinus*. The char originates from potential anadromous char from Lønavatn, Voss river system, south Norway. They were reared at Voss, classified as smolt or immature postsmolt, and released (1973) into the Bolstad fjord in a number of 210.

Recaptured		Year of recapture				
Place	Number	1973	1974	1975	1976	Later
Voss river system	13	4	3	2	1	3
Bolstad fjord	30	13	8	2	5	2

Irrespective of parental type, the char behaved in the same manner after release. Of the resident char, 36 (14.9%) were recaptured during the following 6 yr, all in the lakes of release. Of the smolt, 281 (19.6%) were recaptured. As many as 184 were recaptured in their respective lakes immediately after release. Later in the season and in the three following years, 24 were recaptured in the sea and 73 in the river system, of which 6 showed a marked river–sea growth change in their scales.

This experiment shows that smolt of the northern char, reared and released in the southern nonanadromous area, may migrate to the sea.

RELEASE IN THE BOLSTAD FJORD

The aim of this experiment was to test the capacity for anadromy in offspring of the Salangen chars and the native Løna char when released in an environment free from *P. conostomum*. I expected that the char, released directly into the fjord, would feed on marine items in sufficient quantity to make infection of the ureter fluke during the following winter stay in freshwater less likely.

The Salangen chars originated from the 1960 brood and were released in 1963. The Løna char originated from the 1971 brood and were released in 1973. Both groups were immature and 18–32 cm long, which corresponds to anadromous char in the smolt and postsmolt stages. They were released into the Bolstad fjord in June, within the period of downstream migration of the native brown trout.

Of the 133 Salangen char a total of 42 (31.6%) were recaptured during a period of 5 yr, 40 in the sea and only 2 in the Voss river system. Of the 210 Løna char, 43 (20.5%) were

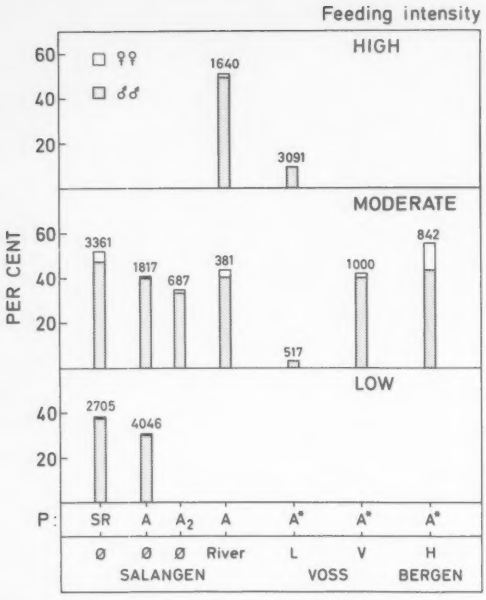

FIG. 7. Fraction of Arctic char *Salvelinus alpinus* maturing at an age of 1+ reared at different feeding intensities. The parents (P) were small resident (SR), anadromous (A), and second generation of anadromous char (A_2), Salangen river system, north Norway (Øvervatn, Ø) and potential anadromous char (A*), Voss river system (Lønavatn, L; Vangsvatn, V), and Bergen (Hauklandsvatn, H), south Norway.

recaptured, 30 in the sea and 13 in the river system (Table 7).

This experiment shows that northern and southern char both in the smolt and postsmolt stage survive a release directly into the sea in the southern nonanadromous area. Further, the recaptures in successive years of the native Løna char indicates that annual migration took place between the home river system and the sea (Table 7).

Genetics and Environment

The rearing experiments (Fig. 7) revealed differences in segregation in offspring from (1) different forms in the same population (Øvervatn, Salangen), (2) the same form from different populations within the same river system (Salangen and Voss), and (3) the same form from different river systems (Salangen, Voss, and Bergen).

Within the same population (Øvervatn, Salangen) a larger percentage of the offspring of the early maturing small resident char (38.1%) reached sexual maturity at an age of 1+ than was the case with the offspring of the late maturing anadromous char (30.8%). This difference was significant at both low ($\chi^2_1 = 38.5$, $P < 0.001$) and moderate feeding intensities ($\chi^2_1 = 63.1$, $P < 0.001$). At moderate feeding the segregation was 52.0 and 40.5% in small resident and anadromous char, respectively.

Offspring of anadromous char from different populations within the same river system (Salangen) segregated slightly differently. The percentage of the offspring of anadromous char from the river reaching sexual maturity at an age of 1+ was slightly higher (43.8%) than for the offspring of anadromous char from the lake (40.5%). The difference, however, was not significant ($\chi^2_1 = 1.5$, $P > 0.2$).

In the offspring of potential anadromous char from different populations in south Norway (Voss, Bergen), the segregation in mature individuals at age 1+ varied considerably. Segregation in offspring of the potential anadromous char from Lønavatn and Vangsvatn (Voss river system) was 3.1 and 42.0%, respectively, the latter corresponding to the segregation in offspring of the Salangen anadromous char. Segregation in the offspring of the potential anadromous char from Hauklandsvatn (Bergen) was somewhat higher, 55.3%, including a comparatively high percentage of females, 12.1%. In the other offspring the proportion of females varied between 0.1 and 4.7%, depending largely on the proportion that reached sexual maturity at age 1+. In the offspring originating from Lønavatn, where only potential anadromous char occur naturally, segregation was particularly low, and none of the females reached sexual maturity at an age of 1+. In all offspring the individuals that matured at an age of 1+ were with few exceptions small resident char measuring 10–22 cm.

The percentage of offspring reaching sexual maturity at an age of 1+ is influenced by feeding intensity. The segregation increased significantly in the offspring of small resident char ($\chi^2_1 = 117.2$, $P < 0.001$) and anadromous char ($\chi^2_1 = 52.3$, $P < 0.001$) from Øvervatn when the feeding intensity increased from low to moderate. A further increase to high feeding intensity, giving an excess of food, increased segregation in the offspring of anadromous char (Salangen river) from 43.8 to 50.5%, and in the offspring of the potential anadromous char (Lønavatn, Voss) from 3.1 to 9.6%. The increase is significant in both anadromous ($\chi^2_1 = 5.7$, $P < 0.05$) and potential anadromous char ($\chi^2_1 = 23.7$, $P < 0.001$).

Increase in feeding intensity also accelerated development in the offspring. At high feeding intensity almost all the males in the offspring of anadromous char (Salangen river) matured at an age of 1+, comprising 49.3% of the total number. The length interval of the males covered the total length interval of both small resident (10.5–21.9 cm) and large resident char (22.0–28.0 cm).

Within their gene pool, the early maturing small resident form and the late maturing anadromous form (Øvervatn) represent the extremes of age at sexual maturity. Offspring of the small resident parents produced significantly more resident individuals and fewer smolts than offspring of anadromous parents, indicating that age at sexual maturity is heritable. The second generation of anadromous parents produced even fewer resident individuals (34.9%), and consequently more smolts than their parents. The difference in segregation was significant ($\chi^2_1 = 6.4$, $P < 0.05$) and indicates a positive effect of selecting for late sexual maturity. On the other hand, a release (1920) of fry of the late maturing anadromous char into Svartebergvatn (Salangen) demonstrates the positive effect of selecting for early sexual maturity, since the

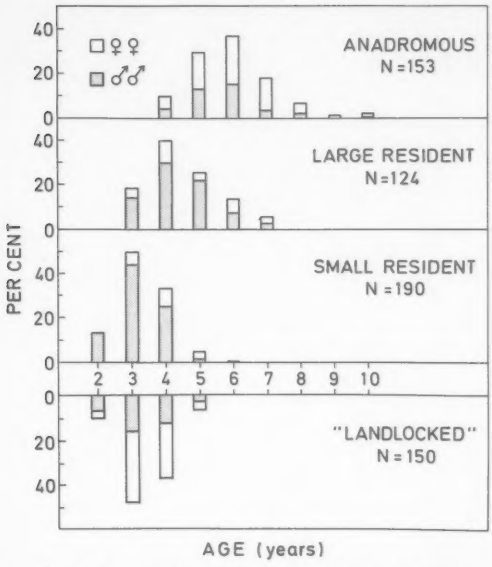

FIG. 8. Age at sexual maturity in the population of Arctic char *Salvelinus alpinus*, Øvervatn (Salangen), consisting of three forms, anadromous, large resident and small resident char, and in "landlocked" char, Svartebergvatn (Salangen). The "landlocked" char are descendants of fry of the anadromous form, released in the lake in 1920.

descendants at the present time (1981) correspond to the early maturing small resident char in age at sexual maturity (Fig. 8). The lake drains via impassable waterfalls into the Salangen river. During the years following the release, smolts were observed to leave the lake and at present only small resident char are left. They mature at a body length of 14–21 cm, and their sex ratio is 1:1.

Discussion and Conclusion

The question whether coexisting forms of Arctic char belong to different populations or to the same gene pool, the "char problem" (Reisinger 1953; Nordeng 1961; Dörfel 1974), is solved by rearing and transplantation experiments. The experiments revealed an identical pattern of segregation in the offspring of northern coexisting small resident, large resident, and anadromous char. During the young stage, parr in each offspring segregated into small resident, large resident, or anadromous char. Each form reproduced itself and the other two forms. Just as in the offspring of northern anadromous char, parr of southern "potential anadromous" parents segregated into coexisting forms present in their respective parental localities. Thus, the coexisting forms of Arctic char belong to the same gene pool as indicated in the investigation on the natural char in the Salangen river system (Nordeng 1961, fig. 19). Reproducing, either in the same or in separate spawning areas, each form gives rise to all three forms as illustrated in Fig. 9.

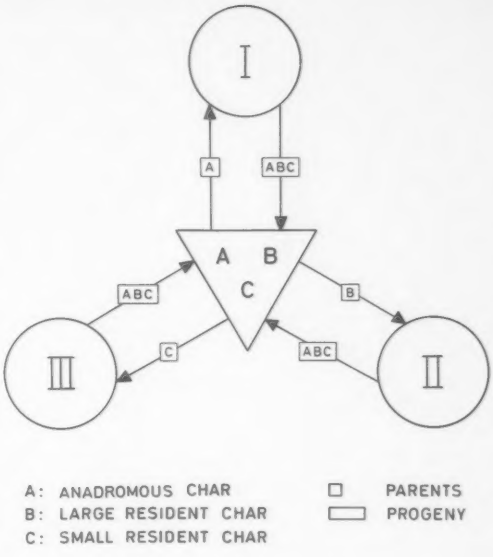

FIG. 9. Reproductive pattern in Arctic char *Salvelinus alpinus* in Øvervatn, Salangen river system, north Norway.

Transplantation experiments confirmed the observed segregation of parr into residents and smolts, and revealed that some resident individuals transformed from one form into another (Fig. 10). Thus single individuals may manifest all three forms during their lifetime, successively attaining the appearance and spawning color of each form. The same phenomenon is observed in natural char (Nordeng 1961, p. 94).

The rearing and transplantation experiments explain the differences in biological characteristics between the coexisting forms of Arctic char (cf. Table 1). In offspring of each form the sex ratio was 1:1. The males reached sexual maturity at a younger age and smaller size than did females. This resulted in a dominance of males in the length interval occupied by the smallest form, and a dominance of females in the length interval occupied by the largest form. The spawning color depended upon body length at sexual maturity.

Within their gene pool, the early maturing small resident form and the late maturing anadromous/potential anadromous form represent the extremes of age at sexual maturity. Offspring of the small resident parents produced significantly more resident individuals and fewer smolts than did offspring of anadromous parents, indicating that age at sexual maturity is heritable. Age at sexual maturity is subjected to rapid selection as the second generation of anadromous parents produced even fewer resident individuals and more smolts than did their parents. This means that a population featuring all three forms incorporates the ability to change into the one or the other extreme form, small resident or anadromous/potential anadromous, respectively. An increase in amount of food

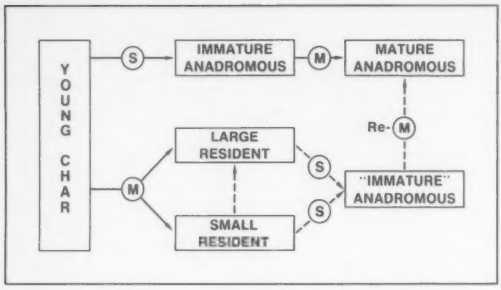

FIG. 10. Segregation (—) and transformation (---) in offspring of small resident, large resident, and anadromous Arctic char *Salvelinus alpinus*, from the Salangen river system, north Norway, revealed by rearing and transplantation experiments. (S) = smoltification, (M) = maturation.

(feeding intensity) accelerates the development in the offspring (shortens the young stage) and increases the proportion of resident individuals. This demonstrates that the pattern of segregation depends both upon genetic constitution and access to food.

In char populations featuring only one form, as in Svartebergvatn (Salangen) and in Lønavatn (Voss), the sex ratio is 1:1. These populations, both originating from anadromous ancestors, seem to be established through natural selection for age at sexual maturity. The two populations exist above waterfalls that prevent upstream migration. In the case of Svartebergvatn, smolts left the lake, so that in the remaining fraction only early maturing small resident char are present. In Lønavatn, smolts do not leave the lake, possibly owing to infection by *P. conostomum*. During the years of isolation intraspecific competition for the restricted spawning area in the lake may have favored the largest individuals, and in the remaining fraction only late maturing potential anadromous char are present.

Transplantation experiments to localities in the northern anadromous area (Salangen and Senja) proved that the capacity for anadromy in northern char had not been affected by water temperature or other abiotic factors during rearing in the nonanadromous area at Voss, and that the fraction of potential anadromous individuals within southern populations exhibit capacity for anadromy when reared under conditions which prevented infection by *P. conostomum*. Transplantation experiments in the southern nonanadromous area (Voss river system and Bolstad fjord outside) revealed that water temperature or other abiotic factors in this area do not prevent anadromous behavior, neither in northern anadromous nor in southern potential anadromous char. In both transplantation experiments the char exhibited annual migration between freshwater and the sea only when released into their respective parental area. This might be explained by orientation towards population-specific pheromones (Nordeng 1977) released from relatives in the parental river system.

The individuals which mature as parr during the young stage may be viewed as the natural resident fraction of anadromous char populations. Anadromous and resident individuals also exist in other salmonids (reviewed by Behnke 1972), for instance in dolly varden char *Salvelinus malma* (Armstrong and Morrow 1980), in masu salmon *Oncorhynchus masou* (Tanaka 1965), and in sockeye salmon *Oncorhynchus nerka* (Ricker 1938; Foerster 1947). In the anadromous fraction of masu and sockeye salmon, females dominate, whereas males dominate in the resident fraction, just as in Arctic char. It is likely that the resident individuals in salmonid populations, comprising either both sexes or males only, represent the same phenomenon. Thus, referring to Salangen salmonids (Fig. 2), the resident individuals, and parr (each of different age) constitute a permanent component of the freshwater bases in their respective migratory systems.

Acknowledgments

First of all I thank my wife, Aase Nordeng. She accepted my devotion to the char, and supported and assisted me throughout this research. I am also indebted to Per Bratland, Institute of Marine Research, Bergen, who assisted me both in the field and in the hatchery. The caretakers at the hatchery, Gunnar Askeland, Bjarne Nedkvitne, and Thoralf Olsen, are also acknowledged for their work. During field work in Salangen, I received valuable help from the Chruickshank family. Ragnvald Andersen and Jostein Skurdal participated in the final preparation of results from rearing and transplantation experiments. I am grateful to Dr Lionel Johnson for critical reading of the manuscript. Financial support was received from the Institute of Marine Research, Bergen; the Norwegian Research Council for Science and the Humanities; the Norwegian Research Council for Agriculture; the Norwegian Fisheries Research Council; and the Directorate for Wildlife and Freshwater Fish. I am indebted to them all.

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Biological Half-lives of Polychlorinated Biphenyl (PCB) Congeners in Whole Fish and Muscle of Rainbow Trout (*Salmo gairdneri*)

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The biological half-life ($T_{\frac{1}{2}}$) of 31 dichloro- to decachloro-biphenyl congeners were monitored for 105 d in adult rainbow trout (*Salmo gairdneri*) that were exposed to a single oral dose. In whole fish $T_{\frac{1}{2}}$ increased from 5 d to no apparent elimination as the number of chlorines on the biphenyl increased. This structure–activity relationship was not as evident in muscle where $T_{\frac{1}{2}}$ ranged from <5 to 127 d. We suggest the decline in muscle resulted from decreasing lipid levels and the redistribution of congeners within the fish. From structure–activity analysis of $T_{\frac{1}{2}}$ in whole fish we conclude that elimination is enhanced for those congeners with lower chlorine content, with no chlorine substitutions in the ortho positions, and those with two unsubstituted carbons that are adjacent (vicinal) on the biphenyl. A significant decline in total PCB content in whole fish, equivalent to a $T_{\frac{1}{2}}$ of 219 d, was partly due to the composition of the PCB mixture administered, and the selective elimination of the lower chlorinated biphenyls.

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On a suivi la demi-vie biologique ($T_{\frac{1}{2}}$) de 31 congénères variant de dichloro- à décachlorobiphényles pendant 105 j chez des truites arc-en-ciel (*Salmo gairdneri*) adultes exposées à une seule dose orale. Chez les poissons entiers, la demi-vie est passée de 5 j à aucune élimination apparente à mesure qu'augmentait le nombre de molécules de chlore attachées au biphényle. Cette relation entre la structure et l'activité n'était pas aussi évidente dans les muscles où $T_{\frac{1}{2}}$ variait de <5 à 127 j. Les auteurs supposent que la baisse dans les muscles a été causée par une diminution des quantités de lipides et la redistribution des congénères dans le poisson. À partir de l'analyse de la relation entre la structure et l'activité de $T_{\frac{1}{2}}$ chez les poissons entiers, ils en arrivent à la conclusion que l'élimination des substances suivantes est accrue dans le cas des congénères à faible contenu de chlore, de ceux sans substitution du chlore dans les positions *ortho* et de ceux avec deux carbones non substitués adjacents (vicinaux) sur le biphényle. Une baisse importante du contenu total en BPC dans les poissons entiers, soit l'équivalent d'une $T_{\frac{1}{2}}$ de 219 j, était due en partie à la composition du mélange de BPC administré et à l'élimination sélective des biphényles chlorés moins saturés.

Received February 4, 1983
Accepted May 24, 1983

Reçu le 4 février 1983
Accepté le 24 mai 1983

POLYCHLORINATED biphenyls (PCBs) are industrial products that can contain up to 209 monochloro- to decachlorobiphenyl congeners (Hutzinger et al. 1974). Aroclor 1254 is one product that has been studied relatively intensively because of PCB contamination of the natural environment (Hansen et al. 1971; Mayer et al. 1977). Its composition can include up to 80 congeners with the pentachlorobiphenyl isomeric group, represented by 22 congeners, making up over half of the total mixture (Sissons and Welti 1971; Albro et al. 1981). In view of this diverse composition, studies are now being focused on the effects of specific congeners in addition to PCB mixtures.

Information on the toxicology and kinetics of congeners in fish is limited to about 20 monochloro- to hexachloro-

Printed in Canada (J7233)
Imprimé au Canada (J7233)

TABLE 1. Whole fish and muscle concentrations of 31 PCB congeners in rainbow trout exposed to a single oral dose at six sample intervals over the 105-d study. Each value represents the mean ± SD of six fish except for values of whole fish at 5 d ($n = 5$). Absorption efficiencies were calculated from estimated concentrations at day 0, extrapolated from levels at 5, 10, and 35 d, and the amount that was orally administered. The half-life of each congener whose decline was statistically significant after adjustment for "growth dilution" is identified by a single ($P < 0.05$) or double ($P < 0.01$) asterisk.

	Whole fish concn., $\mu g \cdot kg^{-1}$, days						Muscle concn., $\mu g \cdot kg^{-1}$, days						Percent absorbed	Half-life, days	
	5	10	25	45	75	105	5	10	25	45	75	105		Whole fish	Muscle
Dichlorobiphenyl	32±14	12±6	ND	2±2	ND	ND	4±6	ND	ND	ND	ND	ND	62	5**	<5**
3,3′	64±24	32±12	6±3	11±14	2±4	2±2	15±10	10±5	2±1	3±4	ND	ND	80	15**	14**
3,5	197±48	152±46	113±44	80±14	51±17	28±11	52±29	55±19	34±5	25±13	12±5	ND	79	40**	20**
2,2′	164±43	130±32	98±33	95±17	80±14	46±16	48±25	50±16	36±6	29±18	16±6	11±8	77	61**	26**
2,3	175±41	144±37	115±38	95±17	72±20	68±21	51±28	55±19	40±5	34±20	20±7	16±10	73	85**	56**
2,5															
Trichlorobiphenyl	83±20	69±17	58±21	50±9	48±8	50±14	23±12	25±9	20±4	18±11	13±4	12±6	77	190**	86**
2,5,2′	96±30	73±19	61±21	56±9	50±13	58±21	30±15	30±11	23±3	20±11	16±4	14±11	78	196**	81**
2,5,4′															
Tetrachlorobiphenyl	83±26	59±22	56±22	35±23	19±18	32±28	25±13	31±22	17±2	10±10	5±5	8±15	68	44**	29**
3,4,3′,4′	89±26	67±18	55±20	47±12	42±8	36±8	27±15	27±11	20±4	17±9	12±4	7±2	73	107**	61**
2,3,2′,3′	91±28	73±21	63±23	55±9	57±10	60±17	28±16	29±11	22±4	21±11	26±5	15±11	78	312**	93**
2,3,4,5	90±21	76±21	64±22	58±10	58±9	63±16	28±14	27±11	21±4	20±12	17±6	14±7	75	365*	107**
2,5,2′,6′	91±20	79±23	71±23	68±12	64±12	68±21	30±17	22±13	23±4	24±14	20±7	20±15	66	430	127**
2,3,2′,4′	81±21	67±21	59±21	56±9	53±10	61±18	28±15	29±11	22±4	22±13	17±6	16±10	74	500	99**
2,5,2′,5′	87±20	74±21	64±21	61±11	61±9	66±17	28±16	29±11	23±4	23±12	17±5	16±10	77	650	108**
2,3,5,6	92±24	75±20	66±23	59±10	62±12	70±20	28±16	29±12	23±5	22±13	18±6	16±12	83	670	108**
2,4,3′,4′	87±22	73±21	64±22	57±10	59±11	69±19	30±17	30±11	22±4	22±12	17±6	16±10	74	890	104**
2,5,3′,5′															
Pentachlorobiphenyl	82±20	66±18	57±22	47±9	46±9	44±12	29±16	28±11	20±4	17±10	13±5	10±6	75	155*	62**
2,3,4,2′,5′	86±26	67±18	61±19	59±13	60±11	66±16	31±16	30±11	23±4	21±12	17±5	16±10	75	820	95**
2,4,6,2′,5′	104±31	86±25	75±26	71±12	75±15	80±19	39±20	37±14	27±5	26±15	21±7	19±12	80	>1000	95**
2,4,6,3′,4′	43±11	35±10	32±12	30±5	31±6	35±9	16±9	15±6	11±3	9±7	7±3	9±6	73	>1000	101**
2,4,6,2′,6′	88±23	73±22	64±23	59±11	62±12	70±18	31±17	30±12	22±4	22±13	17±6	16±10	85	>1000	100**
2,3,4,5,6	61±18	48±16	42±18	41±6	38±10	63±13	25±13	25±10	18±4	18±11	13±5	12±8	78	>1000	85**
2,4,5,2′,5′															
Hexachlorobiphenyl	70±20	75±17	50±17	47±7	48±10	54±15	30±16	31±12	20±4	18±11	14±5	14±10	84	850	81**
2,3,4,5,2′,5′	96±31	78±23	68±26	66±12	64±14	78±22	42±21	49±16	29±5	27±15	20±6	23±16	77	>1000	91**
2,3,4,6,2′,4′	86±27	70±22	60±21	58±10	62±14	68±20	25±18	34±14	23±4	22±13	17±6	17±11	78	>1000	89**
2,3,4,2′,3′,4′	92±22	78±21	73±23	68±12	68±13	80±19	45±22	46±17	31±6	27±16	21±6	20±11	64	>1000	77**
2,4,6,2′,4′,6′	89±26	73±19	62±24	57±11	72±15	70±23	40±22	44±18	29±5	25±15	20±9	19±14	75	>1000	77**
2,4,5,2′,4′,5′	79±23	62±16	56±20	53±9	56±12	66±20	31±17	33±14	21±4	19±12	15±5	16±11	76	>1000	86**
2,3,4,5,3′,4′															
Octachlorobiphenyl															
2,3,4,5,2′,3′,4′,5′	65±21	49±10	43±14	42±8	42±9	51±15	26±14	38±14	26±6	21±15	14±4	15±11	78	>1000	78**[a]
Nonachlorobiphenyl															
2,3,4,5,6,2′,3′,4′,5′	36±12	26±5	23±8	23±5	22±6	29±7	12±6	22±9	17±4	14±11	9±3	10±7	80	>1000	84**[a]
Decachlorobiphenyl															
2,3,4,5,6,2′,3′,4′,5′,6′	29±9	20±4	17±6	17±4	16±5	22±8	6±3	15±7	13±3	13±12	8±4	10±6	63	>1000	122**[a]

[a] $T_{\frac{1}{2}}$ based on concentrations between 10 and 105 d.

biphenyls with most studies restricted to a few biphenyls with an emphasis on 2,5,2′,5′-tetrachlorobiphenyl (Metcalf et al. 1975; Sanborn et al. 1975; Gruger et al. 1976; Guiney and Peterson 1980). More information is available on other animals that indicates that elimination rates among congeners can differ, and some congeners are more toxic than others even within isomeric groups (Poland and Glover 1977; Bunyan and Page 1978; Sparling and Safe 1980).

We monitored the levels of 31 dichloro- to decachlorobiphenyl congeners in rainbow trout (*Salmo gairdneri*) exposed to a single oral dose. Our objective was to use this information to examine the influence of chlorine content and chlorine ring position on congener elimination under similar conditions in fish and to compare the results with observations made on mammalian systems. We also examined the relationship between congener levels in the edible portion (muscle) and whole fish to provide a better understanding of the dynamics of PCB within as well as between the fish and its environment.

Materials and Methods

Laboratory reared rainbow trout averaging 900 g each were maintained at 11 ± 1°C in 660-L circular tanks provided with 8 $L \cdot min^{-1}$ water than was filtered through activated charcoal. Water quality characteristics were previously described by Hodson et al. (1980). Fish were fed to satiation once daily on a commercial dry diet (Rundle Feed Mill Ltd., Palmerston, Ont.).

Five isomeric dichlorobiphenyls, two trichloro-, nine tetrachloro-, six pentachloro-, six hexachloro-, and one each of octachloro-, nonachloro, and decachloro-biphenyl congeners (Table 1) were administered to each fish in one oral dose. Congener standards (Ultra Sci. Inc., Hope, RI) were dissolved in hexane and mixed with capelin fish oil. The hexane was then removed from the PCB−oil mixture using a Snyder 3-stage condenser. Individual concentrations of each PCB congener in the oil ranged from 46 to 261 $\mu g \cdot kg^{-1}$ with the total PCB content of the 31 congeners of 3850 $\mu g \cdot kg^{-1}$. Concentrations were generally higher for the lower chlorinated congeners. The oil mixture was administered by weight, 1 mL oil per kilogram fish, in a gelatin capsule that was inserted into the stomach using a glass tube. Each of the 36 exposed fish was identified by an aluminum opercular tag. A group of 15 control fish was treated in a similar manner with PCB-free oil. Fish were anesthetized with MS-222 during this procedure, but recovered quickly and were feeding within 2 h of treatment. The exposed and control fish were held in separate tanks. The experiment began in early February and was concluded in late May.

A group of six fish was sampled 5 d after the PCB dose was administered, and again after 10, 25, 45, 75, and 105 d. Five control fish were sampled after 5 d, and again after 45 and 105 d. Fish were prepared for chemical analyses according to methods described earlier (Niimi and Cho 1981). Muscle samples representing the edible portion were taken by filleting both flanks from which the skin and fatty areas were removed. The fillets were ground to a homogeneous composition and a 50-g subsample was taken. The excess muscle was added to the remainder of the fish including the skin and fatty areas which was ground and subsampled. After the muscle and fish samples were analyzed for PCB and lipid content, the concentrations for whole fish were mathematically adjusted to account for the subsample of muscle that was removed.

Congener concentrations were determined by capillary gas chromatography using dual fused silica columns after soxhlet extractions with acetone/hexane and H_2SO_4 cleanup (Oliver and Bothen 1982; Oliver and Nicol 1983). Recovery efficiencies were greater than 90% and reproducibility was ±10%. All samples were run in duplicate. Lipid content was determined using a modified chloroform:methanol extraction method which used proportionally less solvent (Bligh and Dyer 1959).

Twenty congeners used in this study were observed as background levels in control fish with most concentrations in the 1−5 $\mu g \cdot kg^{-1}$ range. An analysis of the fish feed indicated the probable source for accumulation. Levels in control fish were subtracted from the respective whole fish and muscle values of exposed fish. The behavior of the congeners examined in this study would, therefore, represent that ingested from the single oral dose.

Absorption efficiencies of individual congeners were calculated by estimating the PCB concentrations in fish at day 0 by extrapolation using the PCB levels observed after 5, 10, and 25 d. These concentrations were then compared to that expected in each fish based on the amount that was orally administered.

The biological half-life ($T_{\frac{1}{2}}$) of congeners was estimated by linear regression analysis of log-transformed data using the measurements of individual fish to determine if the decline in PCB concentrations was statistically significant. A growth coefficient (λ) was applied to adjust the $T_{\frac{1}{2}}$ to account for changes in congener concentrations attributable to "growth dilution" due to increase in fish weight during the study (Niimi and Cho 1981). This procedure was necessary to ensure the $T_{\frac{1}{2}}$ reported would be comparable to adjusted values from other studies conducted on fish maintained under different growth regimes. One exposed fish sampled at day 0 was not included in the analysis because the fish regurgitated the capsule.

Results

Absorption efficiencies among individual congeners averaged 75 ± 6% and varied from 62 to 85% of that ingested by trout (Table 1). There was no trend among isomeric groups to indicate that absorption efficiency is a selective process that can be influenced by the number of chlorines on the biphenyl.

Mean concentrations of individual congeners in whole fish ranged from 29 to 197 $\mu g \cdot kg^{-1}$ and totalled 2708 $\mu g \cdot kg^{-1}$ at the first sample interval (Table 1). The levels among the lower chlorinated congeners generally decreased faster than the more highly chlorinated ones. Total congener content in whole fish was 1653 $\mu g \cdot kg^{-1}$ at the end of the 105-d study. Congener concentrations in muscle were lower than corresponding levels in whole fish with an initial total content of 913 $\mu g \cdot kg^{-1}$ (Table 1). Concentrations of octachloro-, nonachloro-, and decachloro-biphenyl increased about 50% after 10 d, then decreased thereafter with the other congeners in the muscle. Congener concentrations decreased faster in

TABLE 2. Percent lipid (mean ± SD) in muscle and whole fish of control and exposed fish at each sample interval. Ratios (mean ± SD) of average lipid, and of the 21 congener levels whose $T_{\frac{1}{2}}$ was greater than 200 d, in muscle and whole fish at each sample interval are shown.

	Days					
	5	10	25	45	75	105
Percent lipid						Control
Muscle	2.2±1.0			1.4±0.3		1.4±0.7
Whole fish	9.4±2.3			9.6±2.4		10.3±2.8
Exposed						
Muscle	2.1±0.5	2.5±1.4	2.2±0.9	2.3±0.5	1.9±0.8	1.4±0.4
Whole fish	10.6±1.9	12.5±2.9	10.0±3.6	9.2±1.7	8.8±2.7	7.2±1.3
Lipid ratio						
Muscle / Whole fish	0.20±0.07	0.20±0.08	0.22±0.04	0.25±0.0	0.21±0.06	0.19±0.03
PCB ratio						
Muscle / Whole fish	0.42±0.16	0.46±0.11	0.43±0.12	0.40±0.24	0.30±0.06	0.25±0.12

muscle than in whole fish and the rates of decline were similar for most isomeric groups. Total PCB content in muscle was 407 $\mu g \cdot kg^{-1}$ after 105 d.

The growth of exposed and control fish during the 105-d study can be described by the equation:

$$Y = 900_e^{0.00082X}$$

where X represents the number of days, and Y fish weight in grams. Lipid levels, expressed as percent of wet weight, in control fish averaged 1.7% in muscle, and 9.8% in whole fish (Table 2). Lipid levels in the muscle of exposed fish decreased significantly ($P < 0.01$) over the 105-d study. This decline would be equivalent to a growth-adjusted biological half-life of 237 d. Lipid levels in exposed whole fish also declined significantly ($P < 0.01$) during the study that was equivalent to a $T_{\frac{1}{2}}$ of 200 d. There were no mortalities among the fish during the study.

Two factors that would account for the decrease in congener levels are the elimination of the substance by the fish to reduce body burden, and the increase in body weight with no corresponding increase in congener accumulation which would effectively reduce relative concentrations (Niimi and Cho 1981). The latter can become a significant factor in studies where substantial fish growth has occurred. In that case, the estimated half-life could be dependent more on the growth variable than the actual elimination of the substance. Fish used in this study increased in weight by 10% over 105 d. A coefficient (λ) of 0.00082 was applied to account for this weight increase to derive estimates of $T_{\frac{1}{2}}$ that would represent the dilution of the congeners due to fish growth.

Half-lives in whole fish ranged from 5 d to no apparent elimination and generally increased as the degree of chlorination on the biphenyl increased (Table 1). $T_{\frac{1}{2}}$ averaged 41 d and ranged from 5 to 85 d among the five dichlorobiphenyls, and 190 to 196 d for the two trichlorobiphenyls examined. Estimates of about 40–350 d for some tetrachloro- and pentachloro-biphenyls were suggested although most tetra- and penta-, and all of the higher chlorinated biphenyls were not excreted in sufficient quantities to provide a statistically significant estimate of $T_{\frac{1}{2}}$. The relatively short $T_{\frac{1}{2}}$ for 3, 3,′- and 3,5 dichlorobiphenyl, 3,4,3′,4′-tetrachlorobiphenyl, and 2,3,4,2′,5′-pentachlorobiphenyl would suggest the behavior of these congeners could be different from those of other members in their isomeric groups.

$T_{\frac{1}{2}}$ in muscle ranged from <5 to 127 d (Table 1). Values for the dichlorobiphenyls were generally lower than those of the other isomeric groups although the overall response on the elimination of congeners from muscle did not appear to be influenced by the degree of chlorination.

The biological half-lives of the total congener concentrations were also estimated for comparison with the individual congeners. Total levels in whole fish decreased to 1653 $\mu g \cdot kg^{-1}$ after 105 d, which would be the equivalent to a $T_{\frac{1}{2}}$ of 219 d ($P < 0.05$) after adjustment for weight increase. Levels in muscle decreased to 407 $\mu g \cdot kg^{-1}$ at the end of the study to represent a $T_{\frac{1}{2}}$ of 76 d ($P < 0.01$) after adjustment. The $T_{\frac{1}{2}}$ derived for whole fish does not accurately represent an average elimination rate of individual congeners because the decline was primarily due to the rapid elimination of the lower chlorinated biphenyls. In contrast, the 76-d estimate for muscle provided a good approximation for most of the congeners examined.

Discussion

The most serious concern of PCB contamination of the aquatic environment is its potential impact on human health through the consumption of contaminated fish. PCBs have not been established to be a carcinogen in humans although their ability to induce tumors and other histopathological changes and to reduce reproductive success in other animals is well documented (Kimbrough 1974; Goldstein et al. 1974; Allen 1975). Animals can metabolize PCBs by hydroxylation, and some congeners with unsubstituted vicinal carbon atoms may yield an arene oxide intermediary which is a carcinogenic precursor (Jerina and Daly 1974; Roberts et al. 1978).

This study estimated a mean congener absorption

efficiency of 75% which was not influenced by the degree of chlorination. These observations are generally consistent with those of Leib et al. (1974) who reported a 68% retention of Aroclor 1254 fed to trout over a 32-wk period, and those of Bruggeman et al. (1981) who reported efficiencies in goldfish (*Carassius auratus*) of 48–60% among five dichloro- to tetrachloro-biphenyls indicating a lack of structure-related response. Comparative observations on rats are less clear. Bergman et al.(1982) reported absorption efficiencies among five trichloro- to hexachloro-biphenyls decreased from 94 to 28% as the number of chlorines increased. In contrast, Albro and Fishbein (1972) examined the absorption of 20 compounds from biphenyl to hexachlorobiphenyls and reported mean efficiencies of 95% among diets which contained 5, 50, and 200 $mg \cdot kg^{-1}$ PCBs.

The isomeric and cogeneric composition of a PCB mixture that is ingested can differ from that which is retained. Studies among mammals, birds, and fish generally indicate that components of PCB mixtures administered are not all metabolized at the same rate (Grant et al. 1971; Bagley and Cromartie 1973; Hansen et al. 1976). It is evident from this study that there is selective elimination among individual congeners in whole fish which is influenced by chlorine content. This process may change the isomeric composition of a PCB mixture that is retained to one that contains a higher proportion of the more highly chlorinated biphenyls. This can become an important factor that would influence estimates of $T_{\frac{1}{2}}$ for PCB mixtures because of their differences in isomeric composition. Estimates of $T_{\frac{1}{2}}$ reported for mixtures range from 35 d for Aroclor 1242 to no apparent elimination for Aroclor 1254 in salmonids (Leib et al. 1974; Zitko 1977). The $T_{\frac{1}{2}}$ of 219 d in whole fish we observed was due primarily to the retention of the higher and selective elimination of the lower chlorinated biphenyls. This value would have decreased if the mixture administered contained more dichloro-, and trichloro-, rather than pentachloro- and hexachloro-biphenyls, or if the percentages of dichlorobiphenyls used were increased.

Several hypotheses relating the chemical structure to biological activity relationships among congeners that have been based on in vivo and in vitro studies primarily on mammalian systems have been proposed (Matthews and Anderson 1975; Sundstrom et al. 1976; Goldstein 1979). It has been postulated that microsomal enzyme activity can be enhanced by congeners where (1) there are no chlorine substitutions in the ortho positions, and (2) there are chlorine substitutions in the para and at least two meta positions (Goldstein 1979; Parkinson et al. 1980; McKinney and Singh 1981). PCB metabolism may also be enhanced where (3) there are two unsubstituted carbon atoms that are adjacent (vicinal) on the biphenyl (Jensen and Sundstrom 1974; Zell et al. 1978) and where (4) the most lower chlorinated biphenyls will show little or no induction activity (Safe et al. 1982).

All four hypotheses were examined and related to the biological half-lives of congeners in fish observed in this study. The short $T_{\frac{1}{2}}$ of 3,3′- and 3,5-dichlorobiphenyl, and 3,4,3′,4′-tetrachlorobiphenyl in whole fish would support the hypothesis that activity among congeners is enhanced when there are no ortho chlorine substitutions on the biphenyl. These were the only three congeners among the 31 examined that had this chlorine substitution pattern. In contrast, chlorine substitution at both para, and two meta positions was not an important factor that influenced activity in this study. Unsubstituted vicinal carbons can be a contributing factor in lowering $T_{\frac{1}{2}}$. Relatively short half-lives were observed among the five dichlorobiphenyls, two trichlorobiphenyls, 3,4,3′,4′- and 2,3,2′,3′-tetrachlorobiphenyls, and 2,3,4,2′,5′-pentachlorobiphenyl which had unsubstituted vicinal carbons on both phenyl rings. It can also be noted that longer half-lives were observed for several tetrachlorobiphenyls and the other five pentachlorobiphenyls that have unsubstituted vicinal carbons on only one phenyl ring. The hypothesis that lower chlorinated biphenyls will show no induction activity was not supported by this study although the relationship between $T_{\frac{1}{2}}$ and enzyme activity, or lack of, has not been clearly defined. These comparisons would suggest that the behavior among the 31 congeners examined would be consistent with hypotheses 1 and 3, but not 2 and 4. The degree of chlorination on the biphenyl would appear to be the most consistent indicator of biological, or biochemical activity of congeners in fish. These comparisons should be viewed with some caution, however, because the relationships among microsomal enzyme activation and the toxicity, biological activity, and elimination of congeners have not been clearly established. Xenobiotic substances may be excreted as the parent compound, or be metabolized through hydrolysis, oxidation, or conjugation to facilitate elimination (Lech and Bend 1980). Hence a substance that is highly mobile or biologically active may not necessarily be toxic.

Fish appear to be less capable of metabolizing PCBs than other animal groups (Creavan et al. 1965; Hutzinger et al. 1972). Recent studies have postulated that the terrestrial existence of many animals has led to specialized cytochrome and mixed function oxidase enzyme systems that could detoxify substances within the body before excretion (Parke 1981). These enzyme systems are also present in fish although activity levels are lower than those of mammals. The few studies that have examined the presence of metabolites in fish indicate that some congeners can be metabolized. For example, Sanborn et al. (1975) reported 82% of ^{14}C labeled 2,5,2′-trichlorobiphenyl was metabolized to a more polar product in sunfish. Most studies have reported only trace amounts of metabolic products from 2,2′- and 2,4-dichlorobiphenyl, 2,5,2′- and 2,5,4′-trichlorobiphenyl, 2,5,2′,5′-tetrachlorobiphenyl, and 2,4,5,2′5′-pentachlorobiphenyl in several species of fish (Metcalf et al. 1975; Sanborn et al. 1975; Melancon and Lech 1976; Herbst et al. 1978). Other studies report no detectable metabolic products in fish exposed to monochloro- to pentachloro-biphenyls (Hutzinger et al. 1972; Herbst et al. 1978). Hence, we suggest from these studies that many of the higher chlorinated congeners accumulated by fish could be retained as the parent compound.

Qualitative studies on mammals indicate many tetra- to hexa-chlorobiphenyls can induce microsomal enzyme activity (e.g. Goldstein 1979; Parkinson et al. 1980). A quantitative study on the metabolism of four hexachlorobiphenyls in rat indicated a good correlation between $T_{\frac{1}{2}}$, which decreased from 43 to 2 d in the liver, and the ratio of metabolite to parent congener found in bile which increased from 53 to 95% (Matthews and Tuey 1980). Additional studies correlating these in fish are required to achieve a better understanding

of the metabolic consequences of ingesting the different congeners and their relationship to $T_{\frac{1}{2}}$. There are considerable species differences in $T_{\frac{1}{2}}$ among animals, as there are differences in detoxification mechanisms. For example, the $T_{\frac{1}{2}}$ of 2,4,5,2′,4′,5′-hexachlorobiphenyl among mammals has been estimated to be 9, 34, and 370 d in the dog, rat, and monkey, respectively (Matthews and Tuey 1980; Sipes et al. 1982).

Some studies have suggested that lipids, or their components, can play an important role in the redistribution of PCBs (De Freitas and Norstrom 1974; Mitchell et al. 1977; Niimi 1983). Other factors, such as total lipid pool, have been shown to influence contaminant dynamics (Roberts et al. 1977). Our results indicate that the mobilization of congeners from muscle to whole fish was not influenced by chlorine content, except in PCBs with low chlorine content. A comparable study on starved birds indicated that chlorine content did not affect the rate of transfer from muscle to other tissues, there was a nonselective movement of PCBs back into muscle upon refeeding (De Freitas and Norstorm 1974). Lipid levels in whole fish and muscle decreased over the 105-d study in exposed fish (Table 2). The ratio of lipid content in muscle to whole fish remained virtually unchanged although the ratio of PCB concentration in muscle to whole fish decreased from 0.46 to 0.25 for the 21 congeners whose $T_{\frac{1}{2}}$ was greater than 200 d. This could suggest the $T_{\frac{1}{2}}$ for congeners in muscle may not be entirely dependent on changes in total lipid levels in muscle although lipids may play an important role in PCB mobilization.

Other variables such as the large, single, oral, PCB dose administered, and the attaining of equilibrium conditions of congener concentrations and lipid levels could be contributing factors. The measurements indicated that the lower chlorinated congeners attained the highest concentrations in muscle at the first sample interval whereas the nona- and deca-chlorobiphenyl concentrations were highest after 10 d (Table 1). Further studies are required to attain a better understanding of the kinetics of congeners in muscle.

The implications of PCB contamination of the natural environment is most evident in the aquatic ecosystem where the bioaccumulation of persistent contaminants has been an important issue. This study has indicated that the kinetics of PCB congeners in trout is influenced by an efficient nonselective uptake process, and a selective elimination process that is based on the chlorine content, and to a lesser degree, chlorine position of the congener.

Acknowledgments

We thank Lee Durham, Lynne Luxon, and Karen Nicol for their technical assistance during this study.

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An Allocation Model of Growth and Reproduction in Fish

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A simple model is proposed to describe the pattern of allocation of resources into growth and reproduction. This model assumes that there is a fixed amount of surplus energy which may be channeled into either somatic or gonadal tissue. The change in weight or length of a fish can be predicted from this model from the surplus energy and the gonadosomatic index. Evidence is presented that in many species the gonadosomatic index can be assumed to be a constant. Surplus energy can also be estimated by inverting the growth equations. With this information it is possible to examine the consequences on Darwinian fitness of changes in the age at maturity or the allocation to reproduction as measured by changes in the gonadosomatic index. The allocation model is validated using data on the growth of American plaice, *Hippoglossoides platessoides*. It is shown that the reproductive strategy of American plaice cannot be accounted for on the basis of the trade-off between growth and reproduction.

ROFF, D. A. 1983. An allocation model of growth and reproduction in fish. Can. J. Fish. Aquat. Sci. 40: 1395–1404.

Le présent rapport propose un modèle simple permettant de décrire le schème de répartition des ressources pour la croissance et la reproduction. Ce modèle suppose qu'il existe une quantité fixe d'énergie excédentaire qui peut être acheminée vers les tissus somatiques ou gonadiques. On peut prévoir la variation de poids ou de longueur d'un poisson à partir de l'énergie excédentaire et de l'indice gonadosomatique compris dans ce modèle. Selon les données présentées, on peut supposer que l'indice gonadosomatique est constant chez de nombreuses espèces. On peut aussi évaluer l'énergie excédentaire en inversant les équations de croissance. À l'aide de cette information, il est possible d'étudier les répercussions, sur l'état de santé darwinien, des variations de l'âge à la maturité ainsi que la quantité d'énergie canalisée pour la reproduction, calculée d'après les changements de l'indice gonadosomatique. Le modèle de répartition est validé à l'aide de données sur la croissance de la plie canadienne, *Hippoglossoides platessoides*. On démontre que la stratégie reproductrice de la plie canadienne ne peut s'expliquer par l'échange entre la croissance et la reproduction.

Received August 31, 1982
Accepted May 25, 1983

Reçu le 31 août 1982
Accepté le 25 mai 1983

GROWTH and reproduction are important components of fitness. In fish, growth is of particular significance as fecundity is generally an increasing function of body size (Bagenal 1966; Wootton 1979). Energy channeled into the gonads detracts from somatic growth and hence future fecundity (Jones and Johnston 1977; Ware 1980, 1982). There is thus a direct trade-off between growth and reproduction. To study this trade-off we require a model that fits the observed pattern of allocation and can also be used to examine alternative patterns. In this paper I present a simple model that permits such an examination.

There are a variety of models of growth extant in the literature (Parker and Larkin 1959; Taylor 1962; Paloheimo and Dickie 1965; Ursin 1963, 1967; Kruger 1968; Makorova and Zaika 1971; Solomon and Bradfield 1972). I propose that the most convenient model for the analysis of the contribution of the trade-off between growth and reproduction to fitness will possess the following features. First, the parameters of the model must be easily measured under field conditions. Although experiments in the laboratory may tell us much about the process of growth and the pattern of allocation of resources to reproduction, it is essential that any results be readily testable under natural conditions. Second, the model should be as simple as possible. Complexity in models increases the difficulty of obtaining accurate field measures; however, realism must not be sacrificed for the sake of simplicity. Third, the model must be 'open ended' in the sense that if greater complexity is required it can be incorporated and we are not required to resort to an entirely different model. These last two requirements mean that the model must be based on some realistic biological mechanism and not be just an empirical fit to data. Ware (1980) used a simple compartment model to study the consequences of different growth and reproductive patterns on stock and recruitment. The methodology I outline in this paper is based on a similar compartment concept.

Printed in Canada (J7051)
Imprimé au Canada (J7051)

TABLE 1. Some estimates of the exponent β from equation 2 and the mean or range in the gonadosomatic index (γ).

Species	β[a]	γ[b]	Reference
Hippoglossoides platessoides (Scotland)	1	0.15	Bagenal 1957
H. platessoides (Nova Scotia)	1.26	0.09–0.13	MacKinnon 1972
Pleuronectes platessa	1.28	0.09–0.13	Simpson 1951
Platichethys flesus	1	0.18	Hoffman 1971
Clupea h. pallasi	1.27	0.27–0.37	Rabin and Burnhart 1977
Noturus miurus	1	0.15	Burr and Mayden 1982
Perca fluviatilis	1	0.17	Treasurer 1981
P. fluviatilis	1[c]	0.2[f]	LeCren 1951
Lesueurigobius friesii	>1[c]	0.14	Gibson and Ezzi 1978
Rutilus rutilus	1	0.11	Hellawell 1972
Leuciscus leuciscus[d]	>1	0.13–0.22	Mann 1974
Esox lucius	1[e]	0.14[f]	Mann 1976a
Squalius cephalus	1.9[g]	0.03–0.06	Hellawell 1971b
S. cephalus	1	0.05	Mann 1976b
Hysterocarpus traski	>1[h]	0.39[i]	Baltz and Moyle 1982; Bryant 1977
Gobio gobio	>1[j]	0.15[k]	Mann 1980
Cobitis taenia	>1[c]	0.01–0.03	Robotham 1981

[a]If β is not statistically different from 1 then given as 1, otherwise it is the value indicated.
[b]If β differs from 1 the range obtained from the regression equation for the appropriate weight range is given.
[c]γ of first-time breeders kept separate from older fish. Mean value is lower than for later breeders but no indication is given if the difference is statistically significant.
[d]γ increased from age 3 to 6, thereafter remaining constant. Significance of this increase not tested.
[e]Based on a scatter plot of γ on weight. Data not given.
[f]Data not given. γ estimated from figure in paper.
[g]Relationship given in Hellawell (1971b) includes gonads of immature fish. Regression recalculated using only mature fish (i.e. weight 600 g, Hellawell 1971a).
[h]Coefficient not given.
[i]γ not given in paper. Value obtained from Bryant (1977) to indicate the approximate value.
[j]Based on plot of γ on length.
[k]Range not clear, approximate mean value given.
[l]No test given. Figure 12 axis of original paper in error: correct values are 0.01, 0.02, 0.03, 0.04 (Dr P. Robotham, Division of Biology, Derby Lonsdale College, Kedleston Road, Derby DE3 1GB, personal communication).

An Allocation Model

Energy in excess of maintenance requirements may be channeled into somatic or reproductive tissue. This 'surplus energy' (Ware 1975, 1978, 1980) can be measured as the increase in weight of the somatic and gonadal tissues. Mathematically this partitioning can be represented by the equation:

$$(1) \quad W_{t+1} = W_t + \Delta S_t - G_{t+1}$$

where W_{t+1} is somatic weight at age $t+1$, ΔS_t is the maximum potential increase in somatic weight (i.e. surplus energy) at age t, and G is the weight of the gonads at age $t+1$. For annual spawners the age increment would be 1 yr. In general the relationship between G_{t+1} and W_{t+1} is found to follow a power function:

$$(2) \quad G_{t+1} = \alpha W_{t+1}^{\beta}$$

where α and β are constants. Further, fecundity varies as a power function of length, the exponent being about 3 (Bagenal 1966; Wootton 1979). This suggests that β will be generally close to 1. Estimates of β are given in Table 1 for a variety of fish species. The range in β is from 1 to 1.9 with most values lying at or close to 1. Substituting (2) in (1) and rearranging:

$$(3) \quad W_{t+1} = W_t + \Delta S_t - \alpha W_{t+1}^{\beta}$$

$$(4) \quad W_{t+1} + \alpha W_{t+1}^{\beta} = W_t + \Delta S_t$$

$$(5) \quad W_{t+1}\,(1 + \alpha W_{t+1}^{\beta-1}) = W_t + \Delta S_t$$

$$(6) \quad W_{t+1} = \frac{W_t + \Delta S_t}{1 + W_{t+1}^{\beta-1}}$$

Now the gonadosomatic index at age $t+1$, γ_{t+1}, is:

$$(7) \quad \gamma_{t+1} = \frac{G_{t+1}}{W_{t+1}} = \frac{\alpha W_{t+1}^{\beta}}{W_{t+1}} = \alpha W_{t+1}^{\beta-1}.$$

Hence γ_{t+1} can be substituted into equation (6) giving:

$$(8) \quad W_{t+1} = \frac{W_t + \Delta S_t}{1 + \gamma_{t+1}}.$$

If β equals 1, γ_{t+1} is a constant. If β is not equal to 1, the effect of variation in γ will be small provided the range in $1 + \gamma_{t+1}$ is small. Thus in the cases of American plaice, *Hippoglossoides platessoides* (Nova Scotia) and plaice, *Pleuronectes platessa*, the range in $1 + \gamma_{t+1}$ is only 1.09−1.13 and for practical purposes γ might be assumed to be constant. However, for the Pacific herring, *Clupea harengus pallasi*, the variation in $1 + \gamma_{t+1}$ from 1.27 to 1.37 may significantly affect the change in growth and in such cases a constant gonadosomatic index could not be assumed.

The gonadosomatic index and somatic weight are relatively easy to measure. From these can be obtained ΔS_t. Given ΔS_t we may then proceed to examine the consequences of different values of γ on growth and fecundity, and hence fitness. Before general application of this model can be made, it is necessary to demonstrate that the model is valid by comparing the predictions of the model in a case where all of the components of the model can be measured independently. Thus, for example, we could enter ΔS_t and γ into the model and compare the predicted weight with the observed. Alternatively we might estimate γ or ΔS_t from the model and compare it with the observed. Which method we choose depends largely upon the reliability of the observed values of the model components. In the next section the model is validated for American plaice.

Application of the Model to American Plaice

American plaice is distributed widely in the coastal waters of the northwest and northeast Atlantic. In American plaice of St. Mary's Bay, Newfoundland, the change in length between ages 5 and 10 is very close to rectilinear, a slight variation in the theoretical intercept occurring between cohorts (Fig. 1). The growth curves of American plaice in ICNAF divisions 3L and 3N are also close to linear for ages 5−10 (see fig. 7 of Pitt 1975). The minimum age at maturity in St. Mary's Bay American plaice is 11 yr with all fish maturing by age 20 yr (Fig. 1). There is a decrease in the rate of growth associated with the onset of maturity (Fig. 1). I hypothesize that this decrease is due to the allocation of surplus energy into reproductive tissue. Further, on the basis of the linear relationship between length and age of immature fish (ages 5−10) I hypothesize that a fish that does not mature will continue the linear increase in length (the solid straight line of Fig. 1). Weight, W, in American plaice is related to length, L, by the equation $W = 0.0078L^{3.037}$ (Pitt 1964). For practical purposes the exponent can be set at 3. Thus:

$$(9) \quad W_{t+1} + \Delta S_t \propto (L_t + B)^3$$

where L_t is the length at age t and B, the annual increment in length, estimated directly from the published graph (fig. 12 of Pitt 1967) as 2.28 cm/yr. Because the published growth curves are in terms of length it is convenient to recast equation (9) in those terms. Considering both immature and mature fish we have:

$$(10) \quad L_{t+1} = L_t + B, \qquad \text{for ages 5 to maturity}$$

$$(11) \quad L_{t+1} = \frac{(L_t + B)}{(1 + \gamma_{t+1})^{\frac{1}{3}}}, \qquad \text{for mature fish.}$$

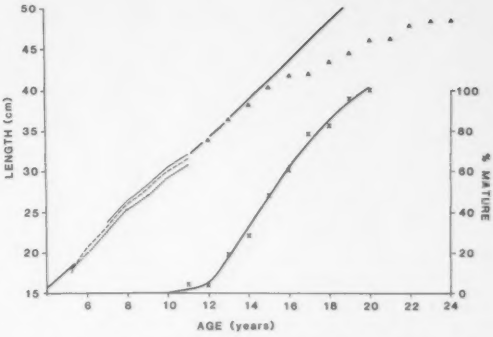

FIG. 1. Growth and maturity curves for St. Mary's Bay American plaice. (—) 1950 year class; (---) 1952 year class; (···) average, all year classes (Data from fig. 12 of Pitt 1967). Age at length data from fig. 8 of Pitt 1967, solid line indicates projected increase in length of immature fish. (×) proportion mature (Data from fig. 8 of Pitt 1964).

The onset of maturity is spread over 10 yr and hence the observed mean length at age t will be given by:

$$(12) \quad \sum_{a=11}^{20} p_a L_{a,t}$$

where p_a is the proportion maturing at ages 11, 12 ..... 20 (estimated from fig. 8 of Pitt 1964 as 2.50, 2.90, 11.40, 16.80, 15.15, 14.85, 13.20, 9.30, 7.90, and 6.00%, respectively) and $L_{a,t}$ is the body length of that proportion of the cohort maturing at age a, referred to as a 'cohort line.'

To compute the gonadosomatic index for a cohort line we require the relationship between γ and body length, and the frequency distribution of the length at age. The relationship between γ and body length can be estimated from the published graph of ovary weight on body length (fig. 7A of Pitt 1964) and the weight/length function. From these we obtain $\gamma = 0.0048L^{0.7568}$. The mean length at age 11 is 32.6 cm at which length the predicted gonadosomatic index is 0.07. However, the value of γ obtained using the graph of gonad weight on age (fig. 7B of Pitt 1964) and the weight/length function is 0.09. The mean gonadosomatic index at age is not equivalent to the gonadosomatic index of the mean length because the gonadosomatic index and length are not linearly related. The only circumstances in which both methods would yield the same result is if there were no variation in length at age, or γ is independent of age or length. For the present analysis the appropriate estimate of γ at age 11 is that derived from the ovary/age plot. However, this plot cannot be used for the older age groups as these comprise cohort lines of different body lengths. The last cohort line matures at age 20 at a predicted length of 53.5 cm. At this length the predicted gonadosomatic index is 0.10. Allowing for the slight underestimation of γ when using the ovary/length relationship we can assume that γ lies approximately between $\gamma = 0.09$ and $\gamma = 0.11$. As discussed previously, variation in the gonadosomatic index γ will only be important if the range in $1 + \gamma$ is large. In the present case the range is only about 1.09−1.11

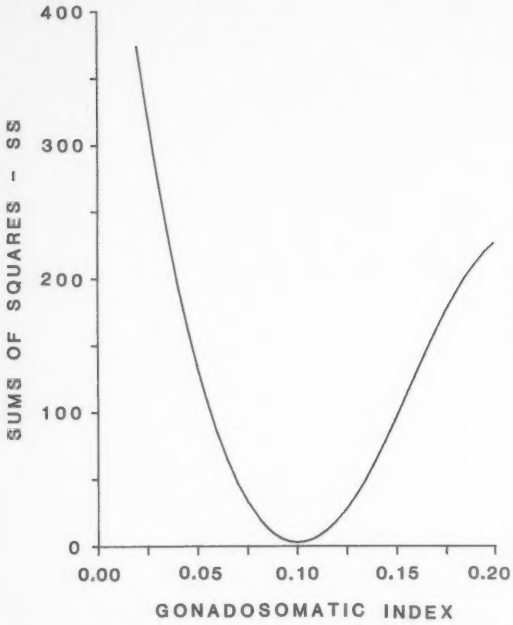

FIG. 2. Relationship between sums of squares between predicted and observed sizes at age (SS) and γ for St. Mary's Bay American plaice.

and we may reasonably set γ at a constant value.

To estimate the appropriate value of γ I adopted a least squares approach, minimizing the quantity:

$$(13)\quad SS = \sum_{i=10}^{24} (\text{observed length at age } i - \text{predicted length at age } i)^2.$$

The sum of squared deviations (SS) was minimized with respect to the two parameters γ, the gonadosomatic index, and L_{10}, the length at age 10 (the year preceding the onset of maturation). γ was varied in steps of 0.001 and L_{10} in steps of 0.1. SS was minimal when $\gamma = 0.10$ and $L_{10} = 30$ cm. The latter value differs very little from the observed mean length at age 10 (30.69 cm). The relationship between SS and γ when $L_{10} = 30$ cm is shown in Fig. 2. There is substantial variation in SS indicating that the value of γ is well constrained. For the observed range in γ of 0.09–0.11, SS is relatively small (Fig. 2) and the predicted lengths differ little from the observed (Fig. 3). The fit between predicted and observed values for $\gamma = 0.1$ is excellent (Fig. 3).

The ability of the allocation model to fit the observed growth curve of American plaice and to predict correctly the value of the gonadosomatic index is strong evidence that the model is a realistic representation of the pattern of allocation of surplus energy to growth and reproduction. We can now predict the variation in size at age associated with different ages at maturity and different levels of allocation to reproduction (i.e. increased or decreased γ). A decrease in the age at maturity or an increase in γ will cause a decrease in the rate of growth. Thus fecundity at some later age will be reduced. Will such a reduction reduce fitness?

The Relative Fitnesses of Different Allocation Patterns

The appropriate measure of fitness depends upon the strength and nature of density-dependent interactions. In a population in which environmental factors are the prime determinants of population fluctuations, the appropriate measure of fitness is the malthusian parameter r (Fisher 1958; Birch 1960; Charlesworth 1980). The situation is more complex when density-dependent interactions are important and there is no single measure that is appropriate in all circumstances. One measure that is appropriate when the populations are stable is the expected lifetime fecundity (Charlesworth 1980; Ware 1982; Dr R. Doyle, Department of Biology, Dalhousie University, Halifax, NS, personal communication). In reality all populations fluctuate and at one time or another are subject to intraspecific density-dependent interactions. Thus the relative fitness of any particular strategy will be in constant flux. The time scale at which fluctuations in population size are relevant in an evolutionary sense will depend upon the lifespan of an organism. For an organism that lives only 1 or 2 yr, fluctuations on the order of decades may be relevant whereas in a long-lived species such as the American plaice the scale may be in the hundreds of years. It is thus difficult in the case of American plaice to measure the degree of population fluctuation on a time scale that is evolutionarily relevant. Therefore, in the present analysis I have examined the effect of different patterns of reproduction on both measures of fitness. The question I address is "does the observed age at first reproduction and allocation to reproduction (γ) maximize fitness"? If the answer is no regardless of the fitness measure used, it is necessary to invoke another factor such as size- or age-dependent mortality.

The malthusian parameter r is calculated by solving the Euler equation:

$$(14)\quad \sum_{t=T}^{\infty} e^{-rt} l_t m_t = 1$$

where t is age, l_t the probability of surviving to age t, m_t is the number of female offspring produced at age t, and T is the age at first reproduction.

For American plaice of St. Mary's Bay in which maturity is spread over 10 yr, equation (14) can be written as:

$$(15)\quad \sum_{t=11}^{\infty} e^{-rt} l_t \sum_{a=11}^{20} p_a m_{a,t} = 1$$

where $m_{a,t}$ is the number of female offspring produced by that proportion of females maturing at age a, and p_a is as previously defined (equation 12). No mortality cost is initially assumed to be associated with reproduction. The term $m_{a,t}$ may be given specific values via the fecundity/length equation (Pitt 1964):

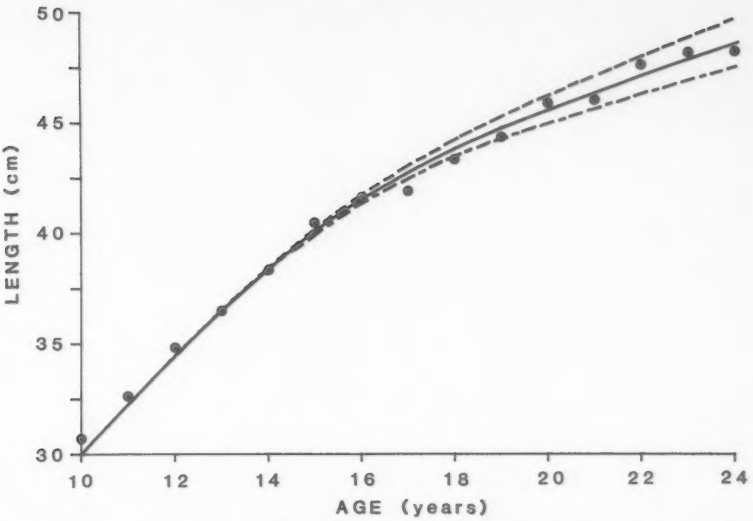

FIG. 3. Predicted and observed growth curves for St. Mary's Bay American plaice. For the predicted curves γ equals, from top to bottom, 0.9, 0.10, and 0.11.

(16) $m_{a,t} = \frac{1}{2}(0.002103)L_{a,t}^{3.1709}$.

Solution of equation (15) is most easily achieved if $m_{a,t}$ is a function of age rather than length as given above. It can be shown (see Appendix A) that the recursive growth equation for mature fish (equation 11) is equivalent to the age-dependent equation:

(17) $L_{t+1} = L_{\max}(1 - e^{-Qt})$

(18) $L_{\max} = \dfrac{B}{(1+\gamma)^{\frac{1}{3}} - 1}$

(19) $Q = \dfrac{1}{T}\ln\left(1 - \dfrac{L_T}{L_{\max}}\right)$

(20) $L_T = A + BT$.

The length at maturity L_T depends upon the age at maturity T and hence there will be 10 separate values of Q corresponding to the 10 successive ages at which American plaice mature.

There are no detailed survival curves for American plaice and hence I have chosen a simple model that incorporates the general pattern associated with fish:

(21) $l_t = qe^{-Mt}$

where q is the proportion surviving the larval period (assumed to be a point event in time) and M, the instantaneous natural mortality rate measured on an annual basis. It is one of the purposes of this study to see whether it is necessary to incorporate age- or size-dependent effects into the survival function. Thus the assumption of a simple but general model is appropriate.

Equation (15) can now be rewritten as:

(22) $$\sum_{t=11}^{\infty} e^{-rt} qe^{-Mt} \sum_{a=11}^{20} p_a \tfrac{1}{2}(0.002103)L_{\max}^{3.1709} \times (1 - e^{-Qat})^{3.1709} = 1.$$

The exponent of the fecundity term differs little from 3: for mathematical convenience and without affecting the conclusions of this analysis a cubic relationship will be assumed. Expanding (22) and using the standard formula for a geometric series:

$$\sum_{n=1}^{\infty} x^{n-1} = \frac{1}{1-x} \qquad |x| < 1$$

we obtain:

(23) $$\sum_{a=11}^{20} CL_{\max} p_a \left(\frac{e^{-T_a K_1}}{1 - e^{-K_1}} - \frac{3e^{-T_a K_2}}{1 - e^{-K_2}} + \frac{3e^{-T_a K_3}}{1 - e^{-K_3}} - \frac{e^{-T_a K_4}}{1 - e^{-K_4}}\right) = 1$$

where:

$K_1 = M + r$
$K_2 = M + Q_a + r$
$K_3 = M + 2Q_a + r$
$K_4 = M + 3Q_a + r$
$C = q\frac{1}{2}(0.002103)$.

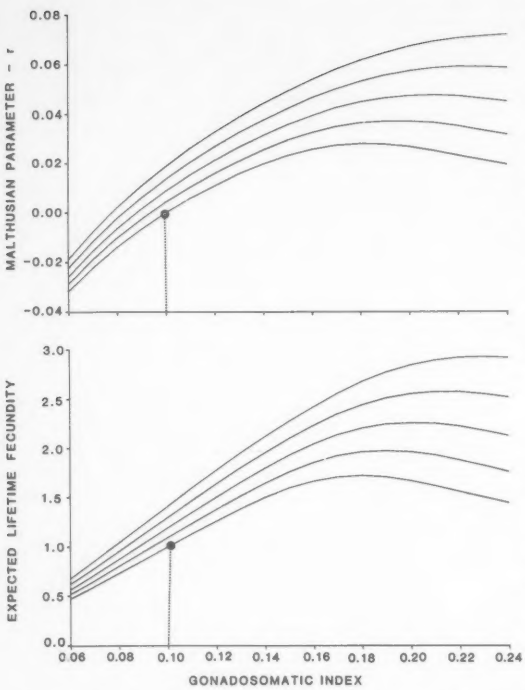

FIG. 4. Relationship between two measure of fitness, the gonadosomatic index γ, and the age at maturity (●, observed combination). (*Top*), Malthusian parameter r. (*Bottom*), Expected lifetime fecundity (female offspring only). For both plots, from top to bottom, the curves shown are for median ages at maturity of 11, 12, 13, 14, 15 (15 = observed age).

The above equation is solved for different values of T_a and γ (which enters via the terms Q_a and L_{max}). The optimum pattern of reproduction is that combination of T_a and γ that gives the highest value of r. To solve (23) requires estimates of C and M. The latter has been estimated by Pitt (1973) as 0.2 but no estimates of the former are available. However, C may be roughly estimated by noting that on average the population should neither increase nor decrease, and hence on average:

$$(24) \quad \sum l_x m_x = 1.$$

It can be shown that fitness depends upon $\ln C$ and hence is reasonably insensitive to variations in C (Roff unpublished data). C was thus estimated by utilizing the observed maturity schedule and $\gamma = 0.1$. The relationship between r and γ for median ages at maturity of 15 (the observed age), 14, 13, 12, and 11 are shown in Fig. 4 (top). In all cases I have assumed the maturity at age curve to be the same shape and have simply shifted the whole curve back the appropriate number of years. It can be seen that by either decreasing the age at maturity or increasing the allocation to reproduction γ, r can be increased. Thus we may conclude that our life history model is deficient in some respect. The second measure of fitness, the expected lifetime fecundity, is equal to the left-hand side of equation 23 with $r = 0$. The expected lifetime fecundity for the same range in γ and medium age at first reproduction is shown in Fig. 4 (bottom). As with the previous fitness measure the analysis indicates that an increase in fitness is obtainable by either earlier maturity or increased reproductive effort. In the case of either fitness measure there is no indication of an optimum near the observed combination of medium age at maturity and γ. To produce an optimum at the observed combination requires the incorporation of an age- or size-dependent mortality function. Substitution of such a component into the model would now permit us to assess quantitatively the relative contribution of the trade-off between growth and reproduction versus survival. This analysis is beyond the scope of the present paper.

Discussion

The model outlined in this paper represents the first step in the development of a model permitting the examination of the effect of alternative strategies of energy allocation on fitness. The model connects the processes of growth and reproduction. The model has been tested using the data on growth of American plaice in St. Mary's Bay, Newfoundland. It both fits the observed growth curve and correctly predicts the value of the gonadosomatic index γ. Obviously more tests are required before the model can be used with confidence to estimate the surplus energy of fish species in which the observed prereproductive growth curve is too narrow to characterize its shape statistically. However, the present results are very encouraging. Further development of the model requires the incorporation of the effect of varying allocation on survival rate.

In American plaice a condition known as 'jellied flesh' has been observed (Templeman and Andrews 1956). The condition is characteristic of mature females and the percentage showing the condition increases with size. It is believed that this jellying is caused by fish metabolizing their somatic tissue to meet the requirements of gonad development. The model presented in this paper predicts that if a fish exceeds L_{max} the allocation to reproduction exceeds the surpus energy: to meet the demands of reproduction somatic tissue must be metabolized. There are two ways in which L_{max} may be exceeded. First, a fish may not mature until a size greater than L_{max}. Second, as L_{max} is a function of γ (equation 18, Fig. 5), an increase in γ may produce a 'new' value of L_{max} that is less than the present size of the fish. For example, suppose $\gamma = 0.1$: at this value L_{max} equals 70.6 cm. At age 24 yr the mean length is 48.6 cm (Fig. 3). Suppose now that a fish increased its gonadosomatic index to 0.18. The 'new' L_{max} is 40.2 cm and the present allocation to reproduction exceeds the surplus energy: consequently gonad development will have to be subsidized by metabolism of somatic tissue. The relationship between γ and L_{max} is shown in Fig. 5: combinations of L_{max} and γ lying above the solid curve are combinations that require the breakdown of somatic tissue to support gonad development. The dashed curve shows the relationship between length and the gonadosomatic index. Thus γ

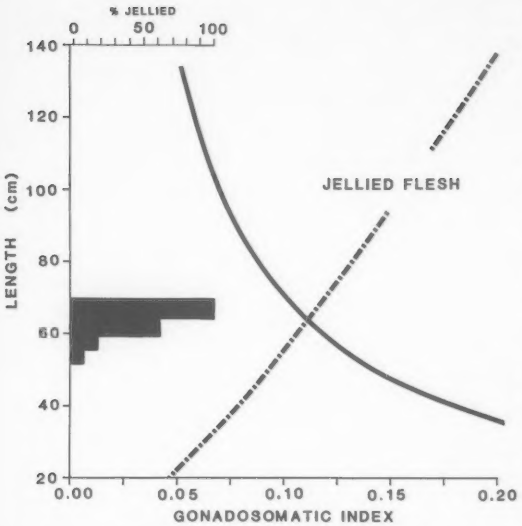

FIG. 5. Solid line: predicted relationship between L_{max} and the gonadosomatic index γ for American plaice of St. Mary's Bay. Dashed line: approximate relationship between γ and length (see text for estimation method). Histogram: frequency of fish from St. Mary's Bay showing 'jellied flesh.' Data from Templeman and Andrews (1956).

increases from ~0.05 at 20 cm to 0.11 at 63 cm. Within this range the surplus energy exceeds the allocation to reproduction and growth continues. Beyond 63 cm this allocation cannot be supported by the surplus energy and the condition of jellied flesh is predicted to occur. The frequency histogram of the percentage jellied flesh according to size category indicates that 71% of fish in the range 60–63 cm have jellied flesh and that 100% of fish in the range 64–67 cm show the condition. Considering the approximate nature of the estimated relationship between length and γ, the correspondence between the predicted length at which the jellied condition should become prevalent and the observed is very satisfactory. The ability of the model to predict the existence of this physiological condition provides further support for its validity.

The analysis of the effects of varying the medium age at maturity and the reproductive effort indicate that there is no local optimum in the region of the observed combination (15 yr and $\gamma = 0.1$). Thus it is necessary to invoke an age- or size-dependent mortality rate. These results are in accord with the hypothesis advanced in Roff (1982) that the age at first reproduction in American plaice is determined in large measure by size-selective mortality.

The reproductive tactics of teleosts are determined in part by the trade-off between growth and reproduction. There may also be a decrease in survival probability associated with reproduction. At present we do not know the extent to which these two components contribute to fitness. The model outlined in this paper enables a first analysis of this problem. The relative importance of survival rates can be assessed by incorporating them into the life history model and their effects on fitness measured by the procedure outlined in the previous section. On the basis of this analysis it can then be decided whether a field examination of survival rates could detect the predicted variation in survival. Clearly, even if an analysis predicts that variation in survival is the determinant of the optimum age at maturity, a field study should only be attempted if the predicted variation is sufficiently high to be detected under natural conditions. Natural selection can operate on small differences and hence it is by no means inconceivable that the important selective mechanisms molding the reproductive strategy of a species may be extremely difficult if not impossible to detect in short-term studies. Thus the careful selection of the species to be studied is of extreme importance.

TABLE 2. Summary of size of male teleosts relative to the female and the associated reproductive characteristics. Full details given in Appendix B.

Size of male relative to female	Territorial behavior[a]	Parental care[b]	Neither
Larger	4	8	0
Equal	1	1	4
Smaller	0	1	26

[a]Male shows territorial behavior but does not show any parental care.
[b]Male builds and defends a nest.

In many species of fish, growth decreases in both sexes at the onset of maturity. The decrease in growth of male fish in general cannot be explained on the basis of the male's allocation to the gonads as this is relatively small. For example, in American plaice and tule perch (*Hysterocarpus traski*) the gonadosomatic indices of the females are 0.1 and 0.39, respectively, but in the males the testes comprise only 2% of the body weight (MacKinnon 1972; Bryant 1977). In fish, fecundity generally increases with size and hence all other things being equal there are selective pressures for continued growth of females. There is no such pressure on males. A hypothesis for the decrease in growth of males is that it is of greater survival value for the males to forage relatively little as foraging may expose a fish to increased risks of predation. In some species such as salmon and some cichlids, there may be intense competition for mates and large males may have the advantage (Hanson and Smith 1967; Perrone 1978), a phenomenon also found in snakes (Shine 1978). There may also be advantages in being large when parental care is involved: larger males may be more able to drive off predators of their eggs and young. To test the hypothesis further that continued growth in males is favored by 'enhanced' reproductive behavior, I classified, where possible, the freshwater fishes of North America into three groups. The first group comprises males that are territorial but show no parental care of the eggs and young. The second group comprises those species in which the males build and guard a nest. The third group consists of those species in which the males do not hold territories and do not care for their progeny. There is a clear association between the relative size of the male and its reproductive behavior (Table 2). Males in the first two categories

are consistently larger than the females whereas males in the last category are consistently smaller. An analysis of the growth patterns of these groups would be of considerable interest. Most particularly an examination of the foraging rates of species with different reproductive modes may shed light on the trade-off between growth and survival.

Acknowledgments

I am most grateful to Drs W. Leggett, M. Lechowicz, R. Peters, and D. Ware for their helpful comments on an earlier draft of this paper. I thank Dr Roger Doyle for a stimulating discussion on measures of fitness. Finally, I would like to thank Dr T. Pitt for useful discussions on the life history of American plaice.

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Appendix A

DERIVATION OF EQUATION (17)

The derivation is most easily shown by proceeding 'backwards' from equation (17):

(1a) $L_t = L_{\max}(1 - e^{-Qt})$.

Rearranging (1a) we have:

(2a) $L_{\max}e^{-Qt} = L_{\max} - L_t$.

Now:

(3a) $L_{t+1} = L_{\max}[1 - e^{-Q(t+1)}]$

(4a) $= L_{\max} - L_{\max}e^{-Qt}e^{-Q}$.

Substituting the left-hand side of (2a) in (4a):

(5a) $L_{t+1} = L_{\max} - (L_{\max} - L_t)\,e^{-Q}$

(6a) $= L_{\max}(1 - e^{-Q}) + L_t e^{-Q}$.

Now recalling equation (16):

(7a) $$L_{t+1} = \frac{B}{(1+\gamma)^{\frac{1}{3}}} + \frac{L_t}{(1+\gamma)^{\frac{1}{3}}}.$$

It is clear that (6a) and (7a) are structurally equivalent. Equation (7a) is valid only at and beyond the age at maturity. Letting T equal the age at maturity we have from (1a):

(8a) $L_T = L_{\max}(1 - e^{-QT})$

from which, by rearrangement we get:

(9a) $$Q = -\left(\frac{1}{T}\right)\ln\left(1 - \frac{L_T}{L_{\max}}\right).$$

From equation (10) the length in the year preceding first reproduction is:

(10a) $L_{T-1} = A + B(T-1)$

and hence the length at first reproduction is:

(11a) $$L_T = \frac{A + B(T-1) + B}{(1+\gamma)^{\frac{1}{3}}} = \frac{A + BT}{(1+\gamma)^{\frac{1}{3}}}.$$

Appendix B

Listing of species in which data are available on the size of the male relative to the female and breeding behavior. Data from Scott and Crossman 1973.

Family	Species	Relative size of male[a]	Parental care[b]
Lepisosteidae	*Lepisosteus osseus*	S	None
Amiidae	*Amia calva*	S	Yes
Clupeidae	*Alosa pseudoharengus*	S	None
Salmonidae	*Coregonus alpenae*	E	"
	C. artedii	S–E	"
	C. hoyi	S	"
	C. kiyi	S	"
	C. zenithicus	S	"
	Prosopium coulteri	S	"
Osmeridae	*Osmerus mordax*	S	"
Hiodontidae	*Hiodon alosoides*	S	"
Esoocidae	*Esox americanus*	S	"
	E. lucius	S	"
	E. muscquinongy	S	"
	E. niger	S	"
Cyprinidae	*Couesius plumbeus*	S	"
	Exoglossum maxillingua	L	Yes (nest)
	Mylocheilus caurinus	S	None
	Nocomis biguttatus	L	Yes (nest)
	N. micropogon	L	Yes (nest)
	Notropis cornutus	L	Territorial
	Pimephales notatus	L	Yes
	P. promelas	L	Yes
	Richardsonius balteatus	S	None
	Semotilus atromaculatus	L	Yes
Catostomidae	*Catostomus catostomus*	S	None
	C. commersoni	S	"
	Hypentelium nigricans	S	"
	Ictiobus cyprinellus	S	"
	Moxostoma anisurum	E	Territorial
Gadiformes	*Lota lota*	S	None
Percopsidae	*Percopsis omiscomaycus*	S	"
Percichthyidae	*Morone americana*	S	"
	M. chrysops	S (slightly)	"
Percidae	*Perca flavescens*	S	"
	Stizostedion vitreum	S	"
	Etheostoma caeruleum	L	Territorial
	E. exile	L	Territorial
	E. flabellare	L	Yes
	E. microperca	S	None
	E. nigrum	L	Yes
	Percina caprodes	E	None
	P. copelandi	L	Territorial
	P. maculata	E	None
Cottidae	*Cottus bairdi*	E	Yes

[a]S, male smaller than the female; L, male larger than the female; E, sexes equal in size.

[b]Yes, male guards eggs and/or young; Yes (nest), male builds nest but abandons it when all eggs are laid; Territorial, male defends territory but does not build a nest.

Estimation of von Bertalanffy Growth Curve Parameters Using both Length Increment and Age–Length Data

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KIRKWOOD, G. P. 1983. Estimation of von Bertalanffy growth curve parameters using both length increment and age–length data. Can. J. Fish. Aquat. Sci. 40: 1405–1411.

Many fish species cannot be aged directly over their full range of lengths. Therefore, to estimate a growth curve, one often uses length increment data from a mark–recapture experiment, supplemented by whatever age–length data are available. I describe a new method for maximum likelihood estimation of the three von Bertalanffy growth curve parameters, using the length increment and age–length data jointly. Also, I describe a likelihood ratio test for determining whether the same growth curve fits both data sets adequately. The von Bertalanffy growth curve can be taken as a predictive regression with either length or age as the dependent variable. Here, age is taken as the dependent variable, as would be appropriate for estimation of age from length, but only minor modifications are necessary for the more common alternative predictive regression of length on age. As an illustration, the techniques are applied to data for southern bluefin tuna, *Thunnus maccoyii*.

KIRKWOOD, G. P. 1983. Estimation of von Bertalanffy growth curve parameters using both length increment and age–length data. Can. J. Fish. Aquat. Sci. 40: 1405–1411.

Pour de nombreuses espèces de poisson, il est impossible de déterminer l'âge en fonction de toute la gamme de longueurs. On utilise donc souvent des données sur l'accroissement de la longueur recueillies à l'aide d'expériences de marquage et de recapture, en plus des données disponibles sur l'âge en fonction de la longueur, pour déterminer la courbe de croissance. Le présent rapport décrit une nouvelle méthode pour l'évaluation de la vraisemblance maximale des trois paramètres de la courbe de croissance de von Bertalanffy, méthode qui utilise conjointement les données sur l'accroissement de la longueur et l'âge en fonction de la longueur. L'auteur présente en outre un test du rapport de vraisemblance visant à déterminer si une même courbe de croissance convient aux deux ensembles de données. On peut considérer la courbe de croissance de von Bertalanffy comme une régression prédictive où soit la longueur ou l'âge constitue la variable dépendante. Dans ce cas-ci, l'âge est la variable dépendante comme il conviendrait pour l'évaluation de l'âge à partir de la longueur, mais seulement des modifications mineures sont nécessaires pour la régression prédictive plus commune de la longueur en fonction de l'âge. Les techniques sont appliquées à des données sur le thon bleu méridional, *Thunnus maccoyii*, comme exercice pratique.

Received November 15, 1982
Accepted May 24, 1983

Reçu le 15 novembre 1982
Accepté le 24 mai 1983

MANY techniques used for assessing the state of exploited fish stocks rely on the availability of age composition data (for example, see Ricker 1975a). A particularly valuable technique for long-lived species is virtual population or cohort analysis (Pope 1972), which depends critically on such data. However, for many species direct aging using scales, otoliths, or other hard parts has not proved successful. In such circumstances, it is necessary to use a growth curve to estimate age compositions, either explicitly or implicitly.

Despite a number of recent papers casting doubt on its suitability and provenance (e.g. Knight 1968; Bayley 1977; Schnute 1981), the von Bertalanffy growth curve remains ubiquitous in the fisheries literature. The usual form of the von Bertalanffy growth curve has length as the dependent variable. However, it is a matter of general statistical principle that if one wishes to estimate age from length by means of a regression equation, then age, not length, should be the dependent variable. Some authors (e.g. Dapson 1980 and others cited therein), while acknowledging this general principle, argue that in some circumstances it may still be appropriate to use inverse prediction with age as the dependent variable. As will be seen later in the example, I do not consider that inverse prediction is appropriate here.

My objective is to present a means of estimating the three von Bertalanffy parameters jointly using length increment data from a mark–recapture experiment and the available age–length data. The techniques are developed with a view to estimating age from length compositions. Consequently they are presented with age as the dependent variable, but only minor modifications are necessary for applications with length as the dependent variable.

The appropriate form of the von Bertalanffy growth curve

Printed in Canada (J7118)
Imprimé au Canada (J7118)

in the context of estimation of age t from length l is

$$(1)\quad t = t_0 - \frac{1}{K}\ln(1 - l/L_\infty).$$

However, if insufficient observations on age at length are available to fit (1) reliably over the range of lengths desired, as is assumed throughout this paper, simultaneous estimation of all three parameters is not straightforward. From mark–recapture experiments, it is possible to obtain data on length at release and recapture of marked fish, and the period at liberty. Then, using the technique introduced by Fabens (1965), the parameters K and L_∞ of (1) may be estimated. For estimating age from length, the appropriate formulation is

$$(2)\quad \delta t = -\frac{1}{K}\ln\left(1 - \frac{\delta l}{L_\infty - R}\right)$$

where δt is the time at liberty, δl is the length increment between release and recapture, and R is the release length. The problem still remains of how to estimate t_0.

Given single or multiple observations on age at length, clearly a point estimate of t_0 can be calculated from (1) conditional on the estimates of L_∞ and K from (2). If there is only a single observation of age at length, or if there are multiple observations of age corresponding to essentially the same length, little more can be achieved. However, frequently there exist observations of age at length for a range of lengths, albeit a restricted one; for example, there are often clear length modes for the first few age classes of the catch of a long-lived species with a restricted breeding season. In these circumstances, the usual practice of conditional estimation of t_0 given L_∞ and K is unsatisfactory on two counts. Firstly, the age at length observations contain some information on L_∞ and K, and no account is taken of this in the conditional estimation. Secondly, the length ranges of the length increment and age at length data rarely coincide. At best, a von Bertalanffy growth curve provides an approximate description of growth over the range of lengths to which it has been fitted, and there is no guarantee that the same von Bertalanffy parameters will be appropriate for both length ranges. Typically, the length increment data correspond to the larger recruited length classes, whereas the age at length data generally are available for smaller fish; indeed the latter data source often includes observations from very small or larval fish (e.g. Poore 1972). Again, such problems are ignored in the conditional estimation procedure.

In this paper, I assume that two data sets are available, one comprising length increment data and the other age at length data. Joint maximum likelihood estimation of all three von Bertalanffy parameters using both data sets is described, under the assumption that departures from (1) and (2) are normally distributed. This procedure efficiently uses all the information on the parameters contained in each data set, and allows reliable estimation of the variance–covariance matrix of the parameter estimates. In addition, a likelihood ratio test is described for explicit testing of the hypothesis that the same von Bertalanffy parameters are appropriate for the two data sets. In the slightly different context of comparing von Bertalanffy growth curves fitted to multiple sets of length at age data, a likelihood ratio test was used by Allen (1968), and a broader exposition of the use of such tests in that context was given by Kimura (1980). The test described here further illustrates the application and usefulness of likelihood ratio tests in fisheries growth studies.

The techniques developed in this paper are illustrated by application to data for southern bluefin tuna, *Thunnus maccoyii*.

Maximum Likelihood Parameter Estimation

Suppose from a mark–recapture experiment we have data from n_1 recaptured fish in the form δt_i, δl_i, and R_i, $i = 1, 2, \ldots, n_1$, where the data for each fish are the period at liberty, the length increment and the release length, respectively. Applying (2), we assume the model

$$(3)\quad \delta t_i = -\frac{1}{K}\ln\left(1 - \frac{\delta l_i}{L_\infty - R_i}\right) + \epsilon_{1i},\ i = 1, 2, \ldots, n_1,$$

where the ϵ_{1i} are assumed to be independent and normally distributed errors, with zero mean and constant variance σ_1^2.

Also, suppose we have further observations of age at length of the form $t_j, l_j, j = 1, 2, \ldots, n_2$. Applying (1), we assume for these data the model

$$(4)\quad t_j = t_0 - \frac{1}{K}\ln(1 - l_j/L_\infty) + \epsilon_{2j},\ j = 1, 2, \ldots, n_2,$$

where the ϵ_{2j} are independent and normally distributed errors, with zero mean and constant variance σ_2^2.

If, in addition, the ϵ_{1i} and ϵ_{2j} are mutually independent, we can write the logarithm of the joint likelihood function of the two samples as a function of the five unknown parameters.

$$\begin{aligned}(5)\quad \Phi(L_\infty, K, t_0, \sigma_1^2, \sigma_2^2) &= -\frac{n_1}{2}\ln(2\pi\sigma_1^2)\\ &\quad - \frac{1}{2\sigma_1^2}\sum_{i=1}^{n_1}\left[\delta t_i + \frac{1}{K}\ln\left(1 - \frac{\delta l_i}{L_\infty - R_i}\right)\right]^2\\ &\quad - \frac{n_2}{2}\ln(2\pi\sigma_2^2)\\ &\quad - \frac{1}{2\sigma_2^2}\sum_{j=1}^{n_2}\left[t_j - t_0 + \frac{1}{K}\ln\left(1 - \frac{l_j}{L_\infty}\right)\right]^2\\ &= \Phi_1(L_\infty, K, \sigma_1^2) + \Phi_2(L_\infty, K, t_0, \sigma_2^2).\end{aligned}$$

The maximum likelihood estimates of the parameters are those that maximize $\Phi(L_\infty, K, t_0, \sigma_1^2, \sigma_2^2)$.

The asymptotic variance–covariance matrix for the parameter estimates is the inverse of the matrix of expected values of the second partial derivatives of $\Phi(L_\infty, K, t_0, \sigma_1^2, \sigma_2^2)$ with respect to the parameters. In practice, this is estimated by evaluating the inverse matrix at the maximum likelihood estimates of the parameters. This approximation generally is considered valid if the log-likelihood surface is approximately quadratic in the region of the maximum.

Testing for Compatibility Between Data Sets

Provided the data are available over a sufficient range, it is possible separately to estimate L_∞ and K from (3) and L_∞, K and t_0 from (4). In such circumstances, both the length increment and age at length data contain information on L_∞ and K. This information is accounted for properly in the joint estimation procedure, as long as the same underlying values of L_∞ and K are appropriate for each data set. However, it is quite possible that the two data sets suggest different estimates of L_∞ and K. This can be examined using a likelihood ratio test.

Setting the problem out in formal terms, suppose for the range of lengths present in the length increment data, the appropriate von Bertalanffy growth parameters are $L_\infty^{(1)}$ and $K^{(1)}$, with log-likelihood function $\Phi_1(L_\infty^{(1)}, K^{(1)}, \sigma_1^2)$. For the range of lengths in the age at length data, suppose the appropriate parameters are $L_\infty^{(2)}$, $K^{(2)}$, and t_0, with log-likelihood function $\Phi_2(L_\infty^{(2)}, K^{(2)}, t_0, \sigma_2^2)$. The compatibility between the two data sets may be examined by testing the null hypothesis

$$L_\infty^{(1)} = L_\infty^{(2)} = L_\infty;\ K^{(1)} = K^{(2)} = K$$

against the alternative that one or both of these parameters differ.

Under the null hypothesis, the maximized log likelihood is $\Phi(\hat{L}_\infty, \hat{K}, \hat{t}_0, \hat{\sigma}_1^2, \hat{\sigma}_2^2)$, which is (5) evaluated at the maximum likelihood estimates of the parameters under this hypothesis. Under the alternative hypothesis, the maximized log likelihood is

$$\Phi_1(\hat{L}_\infty^{(1)}, \hat{K}^{(1)}, \hat{\sigma}_1^2) + \Phi_2(\hat{L}^{(2)}, \hat{K}^{(2)}, \hat{t}_0, \hat{\sigma}_2^2)$$

where the carats indicate maximum likelihood estimates under the appropriate model of the alternative hypothesis.

Then the likelihood ratio test statistic is

$$T = \Phi(\hat{L}_\infty, \hat{K}, \hat{t}_0, \hat{\sigma}_1^2, \hat{\sigma}_2^2) - \Phi_1(\hat{L}_\infty^{(1)}, \hat{K}^{(1)}, \hat{\sigma}_1^2) - \Phi_2(\hat{L}_\infty^{(2)}, \hat{K}^{(2)}, \hat{t}_0, \hat{\sigma}_2^2)$$

and asymptotically, $-2T$ has a χ^2 distribution with 2 degrees of freedom.

On applying the test, if the null hypothesis is rejected in circumstances where it is believed that the underlying assumptions of (3) and (4) are valid, then there is serious cause for concern about the suitability of a single von Bertalanffy growth curve for describing growth over the full range of lengths in the data.

Remark

In his description of the use of likelihood ratio tests for examining differences in von Bertalanffy growth curves fitted to multiple sets of length at age data, Kimura (1980) assumed equality of error variances between data sets. If one were testing for sex differences in growth, or for differences in growth for the same species in different areas, it may well be sensible to assume that the error variances are equal. However, in carrying out these tests, it must be recognized that both the parameter estimates and the likelihood ratio test will be biased if this assumption is violated.

The assumption in Kimura (1980) of equal error variances is not essential. It is simple to modify his tests to allow for different error variances, with the joint likelihood function of the combined samples being simply the product of the individual sample likelihood functions as before, but with a different error variance for each sample. Unfortunately, this destroys the equivalence between the maximum likelihood and least squares estimates and the simple form of the likelihood ratio test statistic proposed by Kimura (1980). However, no essential difficulties arise with this modification. In view of the biases encountered if the assumption of equality of error variances is violated, a specific test of equality of error variances should be carried out before application of the tests proposed by Kimura (1980), even if on theoretical grounds there is no reason to suspect they may be different.

In the procedure described in this paper, there is every reason to expect that the error variances in (3) and (4) differ. This has been allowed for and no test of equality of variances is necessary.

Application to Southern Bluefin Tuna Data

Southern bluefin tuna are taken as prespawning juveniles, generally of ages 2–5 yr, in a pole and line fishery in the Australian coastal zone off Western Australia (WA), South Australia (SA), and New South Wales (NSW). Older fish then become available to the Japanese longline fishery, which operates mainly well offshore in an area extending from 180°W to the mid-Atlantic. The Australian fishery has been reviewed by Murphy (1979) and Majkowski et al. (1981). The Japanese fishery and biology of the species was reviewed by Shingu (1978).

For some tuna species, notably yellowfin (*Thunnus albacares*) and skipjack tuna (*Katsuwanus pelamis*), it was possible to age the fish directly by reading daily growth rings on otoliths (Wild and Foreman 1980). Similar techniques have not been attempted as yet for southern bluefin tuna. In the absence of a suitable age–length key, conversion of catch length distributions to age distributions can only be accomplished through use of an estimated growth curve.

Between 1962 and 1976, as part of a long-term mark–recapture experiment (Hynd 1969), over 20 000 southern bluefin tuna aged between 2 and 4 yr were tagged and released off WA, SA, and NSW (Kirkwood 1981). By 1980 there were 794 recaptures for which the release and recapture dates and lengths are considered reliable (Hearn 1982), and which had been at liberty for at least 250 d. Although the range of release lengths and ages was somewhat restricted, there has been a wide range of recapture lengths, with periods at liberty ranging up to 15 yr and over.

Fishing off SA and NSW is highly seasonal, and in data for each of these fisheries there were clear and well-separated length modes. In WA, the length modes were not as clear and these data were not used. Taking the time of year of catching into account, the modes in SA and NSW clearly represented successive year classes. Previous studies of migration patterns and growth have led to the youngest year class in SA being identified as 2 yr old (Hynd 1969; Hynd and Lucas 1974).

TABLE 1. von Bertalanffy parameter estimates for southern bluefin tuna data.

Data set	L_∞	K	t_0	σ_1^2	σ_2^2	Φ
A. Predictive regression using age as the dependent variable						
Length inc.	209.0	0.125		0.17		−308.21
Modal	214.8	0.133	−0.095		0.025	−102.85
Combined	207.6	0.128	−0.394	0.17	0.031	−402.12

Likelihood ratio test statistic, $-2T = 17.87$ ($P < 0.01$)

Estimated variance−covariance matrix of L_∞, K, t_0 from combined data

$$\begin{bmatrix} 0.312\times10^{1} & -0.409\times10^{-2} & -0.470\times10^{-1} \\ -0.409\times10^{-2} & 0.611\times10^{-5} & 0.841\times10^{-4} \\ -0.470\times10^{-1} & 0.841\times10^{-4} & 0.179\times10^{-2} \end{bmatrix}$$

B. Predictive regression using length as the dependent variable						
Length inc.	185.3	0.155		26.2		−1693.41
Modal	184.2	0.166	−0.036		7.36	−115.36
Combined	184.4	0.157	−0.215	26.2	7.88	−1811.72

Likelihood ratio test statistic, $-2T = 5.89$ ($P > 0.05$)

Estimated variance−covariance matrix of L_∞, K, t_0 from combined data

$$\begin{bmatrix} 0.888\times10^{1} & -0.148\times10^{-1} & -0.100 \\ -0.148\times10^{-1} & 0.260\times10^{-4} & 0.198\times10^{-3} \\ -0.100 & 0.198\times10^{-3} & 0.220\times10^{-2} \end{bmatrix}$$

Here, the modes in SA are taken to correspond to 2-, 3-, and 4-yr-old fish, and those in NSW to 3-, 4-, and 5-yr olds. To take account of differences in timing of the SA and NSW fishing seasons in determining the ages corresponding to the modal lengths, the 'birthday' of the fish was taken to be January 1. Judging from the data presented by Shingu (1978), this date roughly coincides with the period of peak spawning. For each clearly defined mode in the SA and NSW catches, the age corresponding to the modal length was estimated. Catch length frequency data for Australian catches off SA and NSW for the years 1964−79 were used, and 77 age−length "observations" were generated.

It should be noted that more efficient methods exist for the analysis of modes in length frequency data, notably those described by MacDonald and Pitcher (1979) and Schnute and Fournier (1980), and in normal circumstances I would recommend their use. However, a comprehensive analysis of the southern bluefin tuna length frequency data should not only use one of these methods, but also take into account migrations between areas of the Australian coast. This is beyond the scope of this paper. Given the clearness of the modes, the simplistic approach used here to obtain age−length data was deemed adequate for illustration of the estimation procedures developed.

The joint estimation procedure was applied to the length increment and modal age at length data, fitting the predictive regression with age as the dependent variable. The resulting parameter estimates and their estimated variance−covariance matrix are shown in Table 1(*A*). Also given in Table 1(*A*) are the parameter estimates obtained when the von Bertalanffy curve was fitted separately to each data set using (3) and (4), and the value of the ensuing likelihood ratio test statistic. With these data, residual plots revealed no obvious outliers or trends. Further, the likelihood surface near the maximum appeared to be reasonably well approximated by a quadratic surface. This was checked by fitting a quadratic polynomial in the region of the maximum and comparing the maximum function value and parameter estimates obtained for this fit with those obtained from maximizing the full likelihood function.

For the predictive regression with age as the dependent variable [Table 1(*A*)], the likelihood ratio test statistic for testing equality of L_∞ and K between the two data sets was statistically significant. For fish up to 110 cm in length caught in the Australian fishery, the modal age−length data and the curves fitted to the age−length data alone and to the combined data are shown in Fig. 1. Although either curve would have correctly separated catch length frequency data for each year into annual cohorts, that task is much more directly accomplished using the length frequency data themselves. Thus for these fish, the significant test statistic is not an embarrassment. The main difficulty arises for fish over 110 cm, for which no age−length data are available and hence no estimate of t_0. Possible reasons for a significant test statistic and ensuing courses of action in the general case are discussed later. In this example, for fish over 110 cm the combined curve was adopted provisionally, as the estimates of L_∞ and K were very similar for the curves fitted to the combined data and the length increment data alone, and because an approximate variance−covariance matrix for the three parameters was desired for sensitivity analyses. A more comprehensive analysis of the length frequency data is in progress.

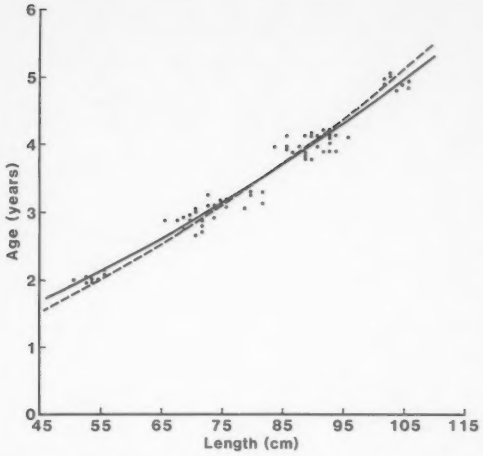

FIG. 1. Age–length data obtained from modes in length frequencies for fish caught off SA and NSW, and von Bertalanffy curves fitted to combined modal and length frequency data (hatched line) and to modal data alone (solid line).

Almost invariably, von Bertalanffy parameter estimates reported in the literature have been calculated using a predictive regression with length as the dependent variable. To compare the parameter estimates obtained when length and age are taken as the dependent variables, estimates for the tuna data when length was the dependent variable are shown in Table 1*B*. The differences between parameter estimates in Table 1 (*A*) and (*B*) are substantial. Certainly, the estimated age at a given length calculated using parameters in Table 1(*A*) differs markedly from that calculated with Table 1(*B*) estimates, and fish over 185 cm cannot be aged at all with Table 1(*B*) parameters. These observations also provide powerful arguments in favor of the general principle enunciated earlier with respect to prediction of age from length. Certainly inverse prediction from a regression with length as the dependent variable is quite inappropriate, at least for larger fish.

Discussion

Written simply as a formula, the von Bertalanffy growth equation takes the form of a functional relationship between the mathematical variables length and age, involving parameters L_∞, K, and t_0. As such, there is no doubt as to the interpretation of the parameters. Such a train of thought often appears to be implicit when a von Bertalanffy growth curve is fitted to a set of data, with the parameter estimates obtained seeming to be taken as estimates of the true parameters of this functional relationship. However, the means almost invariably adopted to calculate these parameter estimates is to fit regression models such as (3) or (4), or their equivalents with length as the dependent variable. Here, particular care was taken to identify these as predictive regressions. As was seen in the tuna example, widely differing estimates can be obtained, depending on whether length or age is the dependent variable. Furthermore, the natural variability in growth between individual fish almost certainly imposes an error structure that is adequately described by neither predictive regression model.

For linear relationships, this topic has been the subject of some controversy, with Ricker (1973, 1975b, 1982) advocating the use of a geometric mean regression. Contrary views have been expressed by Jolicoeur (1975) and by Sprent and Dolby (1980, 1982), who argue against ad hoc use of the geometric mean regression. In the nonlinear case, it seems even clearer that ad hoc solutions will not suffice. The most fruitful approach to obtaining estimates of the parameters of the 'true' relationship may be one in which an attempt is made to model the natural variability directly. Such a model was suggested by Krause et al. (1967) and a similar approach was taken by Sainsbury (1980) to fitting a von Bertalanffy growth curve. However, the nature and number of parameters in these models place heavy demands on the data, which often may not be met in practice.

It seems necessary in most cases to acknowledge simply that the regressions fitted to growth data are predictive regressions. In view of the original application intended for the techniques described in this paper, this conclusion is by no means unwelcome. However, in other examples where the estimated von Bertalanffy parameters are used as input to further calculations, it may be not at all clear that estimates obtained from the predictive regression with length as the dependent variable are the appropriate ones to use. For example, arguably the prominence of the von Bertalanffy growth curve in the fisheries literature is due to its incorporation into the Beverton and Holt (1957) yield per recruit equation, and in a number of implementations of yield per recruit analyses, integrations are performed with respect to age, rather than length. Where the ages must be estimated, it may be more appropriate to use the von Bertalanffy parameters calculated from the predictive regression with age as the dependent variable. This was the view taken by Murphy et al. (1983).

Throughout this paper, I assumed that the error variances are homogeneous within data sets. However, there are many examples that suggest that this may not be a realistic assumption, as noted by Sainsbury (1980). There are two possible ways around this problem. First, the error variances in (3) and (4) can simply be assumed to vary as some function of length. There is no intrinsic difficulty in amending the estimation procedures to allow for this, provided a plausible functional form can be found; the likelihood functions just become slightly more complicated. For age–length data, a suitable function might be determined empirically from a plot of the data, though this may not be so easy for length increment data. Alternatively, one may make a more fundamental change and adopt a model that specifically incorporates individual variability, such as that proposed by Sainsbury (1980). Although ideally this is a more appealing approach, amendment of the estimation procedures along these lines would be much more difficult.

Provided the likelihood ratio test statistic (6) proves to be not significant, the growth curve fitted to the combined data can be used with some confidence to predict age from length. However, in the tuna example it was disconcerting to find that

the test statistic was significant. This raises the question of how to proceed given such an eventuality. There are several possible reasons for a significant test, even given that the data accurately describe growth, and no lack of fit is detected for the individual data sets. First, a von Bertalanffy curve with the same parameters may not fit the data adequately over the entire range of lengths in the combined data sets. Second, the assumptions of the likelihood ratio tests may not be satisfied, and the test therefore may be biased. A third possibility raised by a referee was that the models (3) and (4) may provide estimates of L_∞ and K with different expected values.

The first possible reason is most important when the overlap in length ranges in the two data sets is small. Then it is quite possible that von Bertalanffy curves may fit quite adequately over the length ranges of the separate data sets, and yet a single curve may be inadequate over the combined ranges. This could occur either because fish growth follows a different von Bertalanffy curve for younger or older fish or because a von Bertalanffy curve itself is inappropriate over the full length range. In either case, if lack of fit is not detected over the individual length ranges, there is very little one can do.

Whether or not the first reason applies, it is virtually certain that the assumptions of the likelihood ratio test are not fully satisfied. Although parameter estimates obtained using the predictive regression are valid for prediction, the likelihood ratio test requires that the dependent variable genuinely has no error associated with it. It is quite clear that there is individual variability in fish growth, and attempting to fit (3) or (4) to pooled data for a number of individuals inevitably induces effective variability in the dependent variable, length. Consequently the tests will be biased. This bias is likely to be greatest when the length ranges in the two data sets have the least overlap. In general, the effect on the true, as opposed to the nominal significance level cannot be predicted. However, experience in using this test and tests similar to those proposed by Kimura (1980) on data sets with small overlap in length ranges has led me to suspect that the tests may be more stringent than the nominal level would indicate, although much more work is needed to firm up this suspicion. Note that these problems raised for likelihood ratio tests apply equally to alternative methods for comparing growth curve parameters; I still believe that likelihood ratio tests provide the most effective means of making such comparisons.

The suggested third reason is extremely interesting. Because both (3) and (4) are predictive regressions and length enters the two models in slightly different ways, a difference in expected values of the parameters is quite possible. If there is such a difference, it may result in a falsely significant test statistic even when the two data sets cover similar length ranges. This topic certainly deserves further research.

The aim of my procedure was to obtain estimates of all three von Bertalanffy growth parameters when the primary data set is length increment data. In this context, a significant test statistic (6) leaves one with no demonstrably reliable estimate of t_0, at least for those lengths not found in the supplementary age–length data. Any action at this stage, other than declaring a halt, obviously should be contingent on collection of further data, but possible provisional options are to accept the combined curve for those lengths not found in the age–length data, or estimate t_0 given L_∞ and K from the length increment data, using age data for the largest lengths in the age–length data (assuming for concreteness that the age–length data cover smaller lengths only). The disadvantage of the latter procedure is that estimates of the covariances of t_0 with L_∞ and K and of a prediction interval are rather more difficult to calculate.

To many statisticians, the theory and practice of nonlinear estimation are very familiar. However, this will not be true for all the potential readers of this paper. The joint parameter estimation procedure described can only be carried out using iterative maximization techniques on a computer. Fortunately, users with programming expertise themselves or with access to programming assistance are well catered for by package programs for function maximization (or minimization). Almost all mathematical or statistical program packages available, for example BMD, IMSL, NAG, SPSS, etc., contain suitable versions of such subroutines. With these, implementation of the techniques described should no longer be daunting. A listing of the computer program used to generate the results of this paper is available from me. A Nelder–Mead simplex method (Nelder and Mead 1965) was used for maximization of the likelihood functions.

Acknowledgments

I am extremely grateful to the two journal referees for their constructive and thoughtful suggestions for improvement of an earlier draft of this paper.

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Orthophosphate Turnover Time in Shallow Productive Lakes

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PREPAS, E. E. 1983. Orthophosphate turnover time in shallow productive lakes. Can. J. Fish. Aquat. Sci. 40: 1412–1418.

Orthophosphate turnover times were measured in 18 small and medium-sized lakes in western Canada. Turnover times in eight thermally stratified lakes were similar to those of other Canadian lakes: moderately rapid (up to 42 min) in the spring, increasing to very rapid (3–16 min) during July and August. Turnover times in the shallow (i.e. those which mixed intermittently during summer) productive lakes were far more variable, ranging from 17 min to 17 h in spring and 2 min to 36 h during July and August. For individual shallow lakes turnover times remained constant for particular summers. One shallow lake was studied over two summers. In the first summer, turnover times were extremely slow (7–36 h) and in the second summer they were extremely rapid (2–11 min). Therefore I suggest that the mechanisms controlling nutrient limitation in shallow productive lakes are not constant, and can vary dramatically from year to year.

PREPAS, E. E. 1983. Orthophosphate turnover time in shallow productive lakes. Can. J. Fish. Aquat. Sci. 40: 1412–1418.

Le temps de renouvellement de l'orthophosphate a été quantifié dans 18 petits et moyens lacs de l'Ouest canadien. Le temps de renouvellement dans huit lacs à stratification thermique était semblable à celui observé dans d'autres lacs du Canada, soit modérément rapide au printemps (jusqu'à 42 min) et très rapide en juillet et août (de 3 à 16 min). Le temps de renouvellement dans les lacs productifs peu profonds (c.-à-d. ceux où s'effectue un mixage intermittent pendant l'été) variait beaucoup plus, soit de 17 min à 17 h au printemps et de 2 min à 36 h en juillet et août. Au cours d'un même été il demeurait toutefois constant dans chaque lac peu profond, dont un en particulier a été étudié pendant deux étés. Le temps de renouvellement a été très lent (7 à 36 h) durant la première saison estivale, mais très rapide (2 à 11 min) à la deuxième saison. Ces différences portent donc à croire que les mécanismes qui contrôlent la limitation des bio-éléments dans les lacs productifs peu profonds ne sont pas constants et peuvent varier grandement d'une année à l'autre.

Received December 13, 1982
Accepted May 27, 1983

Reçu le 13 décembre 1982
Accepté le 27 mai 1983

SHALLOW lakes, i.e. lakes which mix intermittently during summer, are often very productive (particularly in terms of primary production). Both rates of primary production and levels of total phosphorus [the nutrient which is usually considered to control production in north temperate lakes (Schindler 1977)] can vary dramatically within years and from year to year in individual shallow lakes (Larsen et al. 1981). The changes in total phosphorus levels observed in these lakes are presumably due to fluctuations in the amount of phosphorus returned from the sediments. Also, the phytoplankton biomass in these lakes often does not respond immediately to reductions in the external phosphorus load (Larsen et al. 1981). Very little is known about phosphorus demand in shallow lakes with large internal loadings.

Phosphorus demand is often assessed by the rate at which carrier-free radioactive phosphate ($^{32}P\text{-}PO_4$) is removed by plankton, defined as orthophosphate turnover time (Rigler 1956). When the orthophosphate turnover time is rapid (i.e. <20 min or <1 h) phosphorus is considered limiting for phytoplankton growth (Lean and Pick 1981; Lean et al. 1983, respectively). Longer turnover times are associated with abundant available phosphorus or physical conditions which hamper growth such as low temperature and insufficient light (e.g. Rigler 1964; Peters 1979; Lean and Nalewajko 1979; White et al. 1982).

Comparative studies of orthophosphate turnover times in North American lakes have been carried out on hard- and soft-water lakes (Rigler 1964), and large and small lakes (Lean and Nalewajko 1979). These studies were carried out in central Canada where most lakes are permanently thermally stratified during summer. In western Canada, shallow productive lakes are common. To manage these lakes for recreational purposes it is necessary to know if phosphorus is in demand. Hence I measured orthophosphate turnover times in water from a total of 10 shallow productive lakes in central Alberta during the open water period. Orthophosphate turnover times

Printed in Canada (J7164)
Imprimé au Canada (J7164)

have not been reported previously for any lakes in this region. Thus, to establish proper controls, turnover times were also measured in water from eight deep lakes in central Alberta.

The Study Lakes

Six lakes were studied in 1980; one of these lakes and 12 new lakes were studied in 1981. The 18 study lakes are situated in glacial till and are located in the boreal mixedwood and lower foothills transition biomes. They are spread out over a large area (7×10^4 km^2) in central Alberta, in the drainage basins of three major river systems (Athabasca, Beaver, and North Saskatchewan rivers). The geographical locations are given in Table 1 (note: Table 1 has 19 entries because two basins in Amisk Lake were sampled).

Ten lakes in this study mixed intermittently during summer whereas 8 were permanently thermally stratified. The lakes in both groups encompassed a wide range of sizes (surface areas 0.70−78, and 0.24−9.3 km^2, respectively), whereas the former were shallower than the latter (mean depths 2.9−6.4 and 6.2−19.4 m, respectively; Table 1). The lakes in the two groups are referred to as shallow and deep, respectively. The study lakes are moderately to highly productive, similar to many lakes off the Precambrian Shield in western Canada, east of the Rocky Mountains. Fifteen of the lakes were studied by Prepas and Trew (1983). The average summer chlorophyll concentration in the shallow lakes was 45 mg/m^3 and in the deep lakes it was 14 mg/m^3 (ranges: 3−150, and 2−51 mg/m^3, respectively). Total phosphorus and chlorophyll *a* concentrations in the euphotic zone were highly correlated in the study lakes (Prepas and Trew 1983). Only two of the lakes, Hastings and Mink, had sufficiently high concentrations of total dissolved solids to be classified as saline (Rawson 1951), and these are only moderately saline (Table 1).

Materials and Methods

Orthophosphate turnover times were measured in 10 shallow lakes; 5 of these lakes were sampled in both spring (May and June) and summer (July and August), 4 were sampled in the summer alone, and 1 in spring alone. Lake Nakamun was the only lake sampled in both 1980 and 1981 (Table 4). Orthophosphate turnover times were measured in eight deep lakes; three were studied in June and during summer, measurements were made one or two times on all eight lakes, including both basins of Amisk Lake (Table 4).

Water samples were collected in the morning (usually between 10:00 and 11:00) at the deepest location in a lake, from either the middle of the epilimnion or the middle of the euphotic zone. The middle of the epilimnion is where high orthophosphate turnover times have been reported for moderately productive lakes (Peters 1975). In the more productive lakes, however, the euphotic zone did not extend to this depth, and in these cases the middle of the euphotic zone was chosen. In situ vertical profiles of temperature and light were measured on each visit to define the depth of the epilimnetic (Hutchinson 1957) and euphotic zones, respectively. The latter was defined as 1% surface-penetrating irradiance as measured with a Lambda LI-185 light meter. Water samples were collected with either a 1.5-L aluminum drop-sleeve water bottle or weighted Tygon tubing; samples collected with the latter were from the middle of either the epilimnetic or euphotic zone to the surface. Samples were placed in 2-L opaque Nalgene bottles. Orthophosphate uptake experiments were performed at a portable station set up next to the lake.

For measurement of orthophosphate uptake by seston and its inverse, turnover time, 300 mL of freshly collected lake water was placed in an Erlenmeyer flask in a water bath in open shade. Carrier-free ^{32}P-PO_4 (obtained from New England Nuclear in dilute HCl) was quickly mixed with the lake water sample and 5-mL aliquots were filtered through 25-mm, 0.45-μm Millipore membrane filters at intervals from 2 to 30 min. To remove residual radioactivity (Lean et al. 1983) the method of Lean and Rigler (1974) for measurement and calculation of orthophosphate uptake was modified slightly. For each sample the tower and filter were rinsed with 5 mL of lake water which had previously been filtered through a 47-mm, 0.45-μm Millipore membrane filter. The experiments were run a maximum of 4 h, and radioactivity was determined with a Beckman LS 9000 liquid scintillation counter. Initially, orthophosphate uptake was calculated from total radioactivity in the filtrate. However, for samples with slow rates of uptake, the resolution for counts on the filtrate was poor. Thus, beginning June 1981, uptake rates were obtained from radioactivity on the filters.

The uptake rate for each experiment was estimated by calculating the % ^{32}P in the filtrate minus % ^{32}P in the asymptote for each sample, converting these numbers to natural logarithms (Lean and Rigler 1974) and finding the slope of the regression of the transformed % ^{32}P in the filtrate on time (min). When biphasic kinetics were observed, the initial slope was used. In experiments with slow uptake rates, no asymptote was reached. As there was a general tendency for the asymptote to increase as the uptake rate decreased, an arbitrary asymptote of 30% was used when none was reached.

Chemical characteristics which have been identified as relevant to phosphorus availability: soluble reactive phosphorus, total dissolved phosphorus, total phosphorus, inorganic nitrogen, total nitrogen, and chlorophyll *a* concentrations, were also measured on water collected from the same location as for the turnover time experiments. Triplicate subsamples were taken from each water sample for chemical analyses. Analyses of samples for total and dissolved phosphorus by the potassium persulfate method (Menzel and Corwin 1965), total Kjeldahl nitrogen by the sulfuric acid−copper sulfate method of D'Elia et al. (1977), ammonia-N by Solórzano's (1969) phenolhypochlorite method, nitrate-nitrite-N by the cadmium−copper reduction method of Stainton et al. (1977), and chlorophyll *a* by the ethanol extraction technique (Bergmann and Peters 1980) were as outlined in Prepas and Trew (1983) and Prepas and Rigler (1982). Soluble fractions were collected by filtration through prewashed 0.45-μm Millipore membrane filters. Soluble reactive phosphorus was determined within 24 h by the molybdenum blue method of Murphy and Riley (1962). Total nitrogen was calculated as the sum of total Kjeldahl nitrogen plus nitrate and nitrite, inorganic nitrogen as the sum of nitrate, nitrite, and ammonia.

To reduce outliers, correlations of various factors with turnover time were done after the data were transformed to $\log_{10}$.

TABLE 1. Background data for the 18 study lakes; location, surface area (A_0), mean depth ($\bar{z}$), and epilimnetic concentration of total dissolved solids (TDS). The lakes were divided into two groups; those which mixed intermittently (shallow) and those which were permanently thermally stratified (deep).

Lake	Lat. (°N)	Long. (°W)	A_0 (km^2)	$\bar{z}$ (m)	TDS (mg/L)
		Shallow lakes			
Battle	52°58′	114°11′	4.80	—	200
Birch	53°45′	114°32′	7.51	4.5	188
Buck	52°59′	114°46′	24.9	—	129
Hasse	53°29′	114°10′	0.81	3.2	274
Hastings	53°25′	112°55′	9.06	3.7	748
Mink	53°31′	114°14′	0.70	3.4	1186
Nakamun	53°53′	114°12′	3.16	3.5	190
Tucker	54°32′	110°37′	7.22	2.9	249
Wabamun	53°33′	114°40′	77.7	6.4	221
Wizard	53°07′	113°55′	2.18	5.0	208
		Deep lakes			
Amisk N	54°35′	112°37′	1.89	10.7	196
Amisk S	54°35′	112°37′	2.27	19.4	203
Baptiste S	54°45′	113°33′	4.43	12.7	195
Eden	53°35′	114°09′	0.41	6.2	128
Ethel	54°32′	110°21′	4.83	6.6	182
Hubbles	53°34′	114°05′	0.45	9.9	390
Moore	54°31′	110°31′	9.30	8.3	476
Narrow	54°35′	113°37′	3.33	14.2	190
Twin	52°55′	114°20′	0.24	15.8	209

TABLE 2. A comparison of replicate ^{32}P-PO_4 derived turnover times (TT_1 and TT_2) and the difference between these replicates in 11 Albertan lakes during 1981. The lakes were divided into two groups: those which mixed intermittently (shallow) and those which were permanently thermally stratified (deep).

Lake	Date	Turnover time (min) TT_1	Turnover time (min) TT_2	Difference $TT_1 - TT_2$ (min)
		Shallow lakes		
Wabamun	July 21	1.6	2.6	−1.0
Nakamun	Aug. 10	2.0	1.9	0.1
Mink	July 20	6.3	4.9	1.4
Nakamun	July 2	9.1	13.3	−4.2
Hasse	July 22	14.0	17.6	−3.6
Birch	May 13	21.2	14.2	7.0
Nakamun	May 20	36.5	37.8	−1.3
Wizard	July 9	45.2	27.4	18
Buck	May 12	388	306	82
Hastings	July 10	616	777	−161
		Deep lakes		
Ethel	Aug. 5	2.7	3.3	−0.6
Moore	Aug. 3	3.8	3.5	0.3
Eden	July 6	8.8	8.5	0.3

TABLE 3. A comparison of ^{32}P-PO_4 turnover times derived from assays for radioactivity on the filter (TT_1) and in the filtrate (TT_2) of the same samples in four Albertan lakes during June 1981. The lakes were divided into two groups: those which mixed intermittently (shallow) and those which were permanently thermally stratified (deep).

Lake	Date	Turnover time (min) TT_1	Turnover time (min) TT_2	Difference $TT_1 - TT_2$ (min)
		Shallow lakes		
Tucker	22	337	345	−8.0
Birch	9	942	758	184
		Deep lakes		
Ethel	24	5.4	7.0	−1.6
Moore	23	22.4	24.1	−1.7

Results

On 13 occasions replicate measurements of orthophosphate turnover time were made from separate lake water samples. The differences between replicates were small (3−50% of the measured values), although the absolute differences tended to increase as the turnover time increased (Table 2). This trend disappeared when the logarithmic transformation was applied to the data. On four occasions the turnover times were estimated from counts both in the filtrate and on the filter for the same experiments. The differences between turnover time estimates from the filter and filtrate were no greater than the differences between true replicates (Table 3). In addition, water samples collected from different epilimnetic depths gave comparable results (Table 4, Narrow July 28 1980 and Wizard June 2 1981). Thus, the techniques used here were repeatable. Changes in the fraction of the sample counted and the portion of the epilimnion sampled did not bias the results.

TABLE 4. Orthophosphate turnover time (TT), soluble reactive phosphorus (SRP), total phosphorus (TP) and total nitrogen to total phosphorus ratio (TN:TP) for water collected at specific depths (z) in 18 Albertan lakes which either mixed intermittently (shallow) or were permanently thermally stratified (deep) during the summer. The ratio of the depth of the euphotic zone to mixing depth ($z_{eu}:z_{mix}$) is indicated.

Lake	Date	z (m)	$\frac{z_{eu}}{z_{mix}}$	TT (min)	SRP (mg/m^3)	TP (mg/m^3)	TN:TP
			Shallow lakes				
Battle	May 12 1981	1	0.5	16.9	0.5	19.8	35.0
Birch	May 13 1981	1	0.7	17.7	2.6	27.2	48.4
	June 9 1981	4	1.4	850	4.8	37.8	36.0
	July 27 1981	0–1	0.9	655	16.1	70.8	19.7
Buck	May 12 1981	1	0.5	27.5	0.4	26.9	29.6
	July 15 1981	0–3	0.4	347	5.4	25.1	28.8
Hasse	July 22 1981	0–5	1.2	15.8	1.9	21.9	50.2
Hastings	June 8 1981	0–2	0.4	1036	—	134	23.6
	July 10 1981	0–1.4	0.3	696	23.1	161	26.8
	July 23, 1981	0–1	0.4	1061	53.2	163	31.0
Mink	July 20 1981	0–3	0.7	5.6	1.6	30.7	34.5
Nakamun	July 10 1981	2	0.2	434	17.5	105	13.1
	July 30 1980	0.5	0.3	1448	68.8	205	7.1
	Aug. 19 1980	0.25	0.2	2171	80.9	190	8.2
	May 20 1981	1	0.4	37.1	2.3	80.5	17.6
	June 10 1981	0.5	0.2	26.8	4.9	133	14.8
	July 2 1981	0.5	0.2	11.2	—	—	—
	July 28 1981	0–1	0.4	4.9	3.7	—	—
	Aug. 10 1981	0–1	0.3	2.0	6.5	131	26.8
Tucker	Aug. 4 1981	0–1	0.2	12.3	4.0	56.9	18.4
Wabamun	July 21 1981	0–2	—	2.1	4.8	34.3	29.3
Wizard	June 2 1981	2	0.8	146	1.0	25.6	33.7
	June 2 1981	0–5	0.8	116	1.6	25.6	33.6
	July 9 1981	0–3	0.7	36.3	2.0	32.2	28.5
			Deep lakes				
Amisk N	July 22 1980	2	—	5.3	4.1	33.7	25.4
	Aug. 12 1980	1	0.4	15.5	2.0	42.6	27.2
Amisk S	Aug. 12 1980	1	0.4	9.7	1.9	35.0	28.8
Baptiste S	July 23 1980	2	—	14.9	1.6	46.5	17.0
	Aug. 13 1980	1	0.3	10.4	1.9	94.1	12.4
Eden	June 3 1981	4	2.0	41.8	1.4	17.4	43.5
	July 6 1981	0–3	2.4	8.6	2.0	14.7	35.9
Ethel	June 24 1981	0–4	—	6.2	1.1	18.4	41.6
	Aug. 5 1981	0–4	0.8	3.0	4.9	16.0	54.4
Hubbles	July 9 1980	2	1.8	2.7	0.7	15.0	45.1
	Aug. 19 1980	1	1.7	3.4	0.6	16.7	50.5
Moore	June 23 1981	1	1.0	23.2	0.8	19.9	53.1
	Aug. 3 1981	0–4	1.0	3.7	2.9	22.0	50.9
Narrow	July 28 1980	1	1.8	3.1	0.8	11.3	—
	July 28 1980	3	1.8	4.0	0.7	11.4	49.4
Twin	July 14 1980	2	2.2	5.7	2.8	11.6	42.0
	Aug. 7 1980	1	1.7	10.1	1.3	9.1	45.9

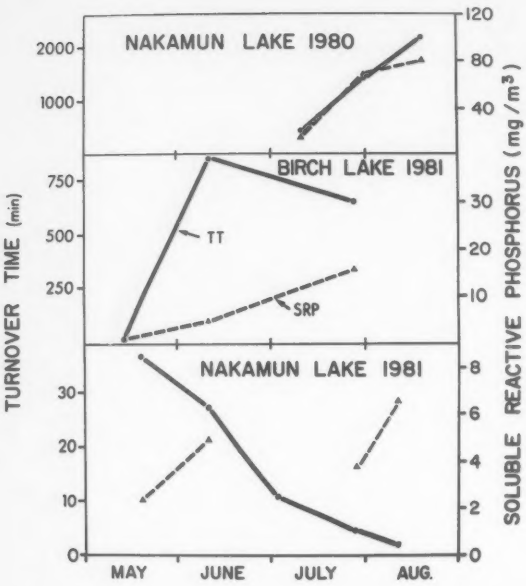

FIG. 1. Changes in turnover time (TT) and concentration of soluble reactive phosphorus (SRP) during the open water period in two shallow productive lakes in central Alberta.

Substantial differences in turnover times were found between experiments carried out beside the lake and in the laboratory, even when great care was taken to avoid temperature changes and light shock. On June 3, 1981, a turnover time experiment was carried out beside Lake Eden, and then 3 h later on identical water back at the laboratory (50 km from the lake). The turnover time at the lakeside was 42 min and in the laboratory it was 9 min, a difference severalfold greater than comparable replicate samples (Table 2). Thus the only turnover time estimates used were those measured beside the lake. The replicates reported in Tables 2 and 3 were averaged to give a single estimate of the turnover time.

In the shallow lakes, orthophosphate turnover times varied between lakes. Spring turnover times varied from rapid to slow (17 min−17 h). In summer, the differences in turnover times were even greater, ranging from 2 min to 36 h. Temporal patterns in open water turnover times varied in five lakes where measurements were made in more than one season. In Birch and Buck lakes, the turnover times were much slower in summer (6−14 h) as compared to spring (18−28 min) as illustrated with data from Birch Lake in Fig. 1. In one lake, Hastings, the turnover times were extremely slow throughout the study period (11−18 h). In the two other lakes, Nakamun during 1981 and Wizard, the turnover times were more rapid in the summer (2−11 min and 36 min, respectively), than in spring (27−37 min and 116−146 min, respectively) as illustrated by Nakamun Lake 1981 in Fig. 1.

Summer turnover times measured over two summers in Lake Nakamun were very different. During 1980 turnover times were consistently slow, ranging from 7 to 36 h, whereas in the summer of 1981 they were extremely fast, ranging from 2 to 11 min (Fig. 1). Spring turnover times varied from moderately fast (42 min) to rapid (6 min). Contrary to the results reported for the shallow lakes, summer turnover times were all uniformly rapid (3−16 min) in the deep lakes. In the three lakes where both spring and summer turnover times were measured, summer turnover times were faster than spring turnover times.

To explain the differences in orthophosphate turnover times in the study lakes, I ran correlations on turnover time and seven factors which have been related to nutrient availability, i.e. soluble reactive phosphorus (SRP), total dissolved phosphorus, total phosphorus (TP), inorganic nitrogen, total nitrogen (TN), and chlorophyll *a* concentrations, and the TN to TP ratio. Only SRP ($n = 39$, $r^2 = 0.45$, $P < 0.0001$; Fig. 1) and TP ($n = 39$, $r^2 = 0.40$, $P < 0.0001$) were significantly correlated with turnover time. However, this relationship held only for high phosphorus values, as illustrated in Fig. 1. For the lakes where SRP was less than 8 mg/m^3, SRP and orthophosphate turnover time were not correlated ($n = 33$, $r^2 = 0.01$, $P > 0.68$), whereas SRP and turnover time were strongly correlated in lakes where SRP was more than 8 mg/m^3 ($n = 6$, $r^2 = 0.89$, $P < 0.01$).

Discussion

The summer orthophosphate turnover times reported for the deep lakes (Table 4) are very similar to those reported for Lake Memphremagog, Quebec (Peters 1979) and just slightly slower than reports for similar-sized lakes in Ontario (Rigler 1964; Lean and Nalewajko 1979; White et al. 1981). In addition the seasonal patterns were similar to those reported elsewhere (Rigler 1964; Peters 1975).

Although six of the shallow lakes (Hasse, Mink, Nakamun 1981, Tucker, Wabamun, and Wizard) showed patterns similar to the deep lakes, four others (Birch, Buck, Hastings, and Nakamun 1980) did not. In the latter, summer turnover times were very slow.

Two explanations have been suggested for slow summer orthophosphate turnover times. First, when the mixing depth is much deeper than the euphotic zone, such as in the western basin of Lake Erie, Lean and Nalewajko (1979) suggest that phytoplankton are light-limited rather than nutrient-limited. Second, lakes with slow orthophosphate turnover times, such as in New Zealand, are considered nitrogen rather than phosphorus-limited (White et al. 1982). Neither of these explanations fits the unusual dynamics observed in the shallow productive lakes in this study.

This shallow lakes in this study varied from moderately to extremely productive (Table 4) and had standing crops of phytoplankton proportional to the total phosphorus levels (Prepas and Trew 1983). In most of these lakes the euphotic zone was much shallower than the mixing zone, but this fact did not appear to influence orthophosphate turnover time (Table 4). For example, in Lake Nakamun the euphotic zone seldom extended below 2 m, and the mixing zone varied from 3 m to the entire water column in both summers. Yet the turnover times in Lake Nakamun varied from extremely slow in the summer of 1980 to rapid in 1981.

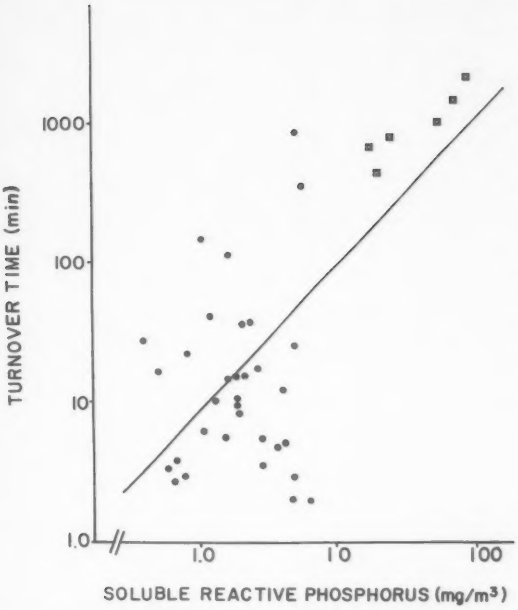

FIG. 2. Orthophosphate turnover time plotted against soluble reactive phosphorus in water collected from lakes in central Alberta. Solid circles indicate samples with less than 8 mg/m^3 SRP and solid squares indicate water samples with more than 8 mg/m^3 SRP. The solid line is the least squares linear regression line.

It is unlikely that nitrogen limitation is responsible for the extremely slow orthophosphate turnover times measured in four shallow lakes (Birch, Buck, Hastings, Nakamun 1980). Total nitrogen to total phosphorus ratios were very high in three of these lakes (20–36), and in the fourth, Lake Nakamun 1980, they ranged from 7 to 13 which is not considered low enough to indicate nitrogen limitation by some authors (Schindler 1977). In addition Murphy and Brownlee (1981) suggest that nitrogen limitation is a rare event in prairie lakes, similar to those in this study.

In this study, orthophosphate turnover time was positively correlated with SRP. This correlation results from two factors: (1) in the lakes with more than 8 mg/m^3 SRP, turnover time and SRP were strongly correlated, (2) turnover time was generally faster in lakes where SRP levels were low than in lakes where SRP levels were high (Fig. 2), although turnover time and SRP were not correlated in lakes where SRP levels were less than 8 mg/m^3. These results are consistent with those reported by White et al. (1981) on other small and medium-sized Canadian lakes, although their study contained only one lake with more than 8 mg/m^3 SRP. Slow turnover times were also reported for the three lakes with more than 6 mg/m^3 SRP in Peters and MacIntyre's (1976) study of East African lakes. The strong correlation between orthophosphate turnover time and high concentrations of SRP in this study suggests that SRP (>8 mg/m^3) estimates the amount of available phosphorus. The distribution of SRP and orthophosphate turnover time values in Fig. 2 is consistent with the hypothesis that SRP overestimates orthophosphate at low concentrations.

Apparently shallow lakes are phosphorus-limited only some of the time, and summer phosphorus availability can vary dramatically in one lake over different years. Yet total phosphorus and chlorophyll *a* levels are closely correlated in these lakes (Prepas and Trew 1983).

Further studies are required to determine the causes of this transient phosphorus deficiency during summer in shallow lakes. A clue to this phenomenon may rest with the variable nature of the exchange of phosphorus between sediments and surface waters. The sediments can be a significant phosphorus source in shallow lakes at irregular periods during summer. The amount of phosphorus returned from the sediments could vary considerably not only between lakes, but in the same lake over different years. Further studies of orthophosphate turnover times in shallow lakes should include careful monitoring of sediment–phosphorus release and phosphorus deficiency in various particulate fractions in the surface waters.

Acknowledgments

I thank G. Hutchinson, J. Vickery, and I. C. Wisheu for their assistance with data analysis and manuscript preparation; L. Alexander, M. Diamond, and J. Vickery for long hours spent in the field; R. H. Peters and C. J. Strobeck for their comments on the manuscript; and the Alberta Recreation, Parks and Wildlife Foundation and the Natural Sciences and Engineering Research Council of Canada for financial support in the form of a grant and operating grant, respectively.

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Iron in Eutrophic Clear Lake, California: Its Importance for Algal Nitrogen Fixation and Growth

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Clear Lake, California, is warm, shallow, polymictic, and eutrophic. During 1975, levels of dissolved (<0.45 μm) iron in all three basins of Clear Lake were always low (15–30 $\mu g \cdot L^{-1}$) and decreased to 2 $\mu g \cdot L^{-1}$ during the major bloom of *Aphanizomenon flos-aquae*. Nitrogen fixation (acetylene reduction) rates of the blue-green algal populations were stimulated as much as 500% above control levels by iron additions in laboratory and in situ large-volume bioassays. Carbon fixation rates and chlorophyll *a* levels were also significantly stimulated by iron additions, but usually less rapidly and to a lesser extent than N_2 fixation. Additions of nitrate stimulated carbon fixation and chlorophyll production but inhibited increases in nitrogen fixation. Phosphate additions either had no effect or produced a mixture of stimulation or depression of all three variables. The bioassays indicate that the growth of blue-green algae and other algae in Clear Lake is usually directly limited by combined nitrogen and occasionally by iron or phosphorus. Low iron levels aggravate the effects of low nitrogen by limiting nitrogen fixation, thus reducing blue-green algal growth.

WURTSBAUGH, W. A., AND A. J. HORNE. 1983. Iron in eutrophic Clear Lake, California: its importance for algal nitrogen fixation and growth. Can. J. Fish. Aquat. Sci. 40: 1419–1429.

Polymictique et eutrophe, le lac Clear en Californie est chaud et peu profond. En 1975, les niveaux de fer dissous (<0,45 μm) dans les trois bassins du lac sont restés peu élevés (15 à 30 $\mu g \cdot L^{-1}$) et ont chuté à 2 $\mu g \cdot L^{-1}$ pendant l'efflorescence de *Aphanizomenon flos-aquae*. Les taux de fixation de l'azote (réduction de l'acéthylène) par les populations d'algues bleues-vertes ont été portés jusqu'à 500% au-dessus des niveaux étalons par des additions de fer au cours de bio-essais sur de grands volumes en laboratoire et sur le terrain. Les taux de fixation du carbone et les niveaux de chlorophylle *a* ont aussi été grandement stimulés par l'apport de fer mais en général moins rapidement et d'une façon moins importante par rapport à la fixation du N_2. Les apports de nitrate ont augmenté la fixation du carbone et la production de chlorophylle mais ont inhibé l'accroissement de la fixation de l'azote. Les additions de phosphate n'ont eu soit aucun effet ou ont produit un mélange de stimulation ou d'abaissement des trois variables. Selon les résultats des bio-essais, la croissance des algues bleues-vertes et des autres algues dans le lac Clear est d'ordinaire directement limitée par l'azote combiné et à l'occasion par le fer et le phosphore. De faibles niveaux de fer augmentent les effets de concentrations peu élevées d'azote parce qu'ils en limitent la fixation, ce qui entraîne une diminution de la croissance des algues bleues-vertes.

Received December 6, 1982
Accepted May 27, 1983

Reçu le 6 décembre 1982
Accepté le 27 mai 1983

THE relative importance of nitrogen, phosphorus, and other nutrients for algal growth has received considerable attention in studies of freshwater systems. Schindler (1976, 1977) argues that because blue-green algae are capable of fixing abundant dinitrogen (N_2), nitrogen will seldom become limiting to algal populations, and phosphorus supplies will control productivity. This view gains support from the observation that blue-green algae, cultured in appropriate media, can fix sufficient dinitrogen to attain vigorous growth. However, results from field studies often indicate that nitrogen, not phosphorus, is the primary nutrient-limiting algal growth in a variety of freshwater and marine systems (e.g. Gerloff and Skoog 1957; Ryther and Dunstan 1971; Strickland 1972;

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Printed in Canada (J7148)
Imprimé au Canada (J7148)

Viner 1973; Goldman 1974).

What then keeps blue-green algae from fixing sufficient dinitrogen in these systems to overcome the nitrogen limitation? Eyster (1970) demonstrated that nitrogen fixation in blue-green algae requires large amounts of iron, and Murphy et al. (1976) showed an increase in iron uptake of algal populations in Lake Ontario during periods of nitrogen fixation. Elder and Horne (1977) concluded that iron was an important nutrient controlling nitrogen fixation in a freshwater reservoir. Consequently, limitation of nitrogen fixation by low iron levels is suggested for freshwater lakes and perhaps for the oceans where iron occurs in very low concentrations.

Here we report the importance of iron and other nutrients in controlling nitrogen fixation and growth of algae in eutrophic Clear Lake, California. Iron levels in the lake are often low and early studies suggested that fixed nitrogen and perhaps iron limited algal growth (Goldman and Wetzel 1963; Javornicky et al. 1973; Miller et al. 1974). In Clear Lake, a bloom of *Aphanizomenon* fixes large quantities of nitrogen each spring but collapses before phosphorus has been exhausted (Horne and Goldman 1972; Lallatin 1975; Horne unpublished data). We therefore hypothesized that nitrogen fixation and consequently blue-green algal growth was limited by iron. We tested this hypothesis during 1975 and 1976 in Clear Lake, principally by the use of nutrient addition bioassays. We also measured iron concentrations, nitrogen fixation, algal biomass, and physical factors in the lake to determine if correlations could be established between these parameters.

Methods

Study Area

Clear Lake is located in the semiarid coast range of northern California, USA (121°W, 39°N). In this region, summers are dry and warm. Winters are cool and most of the rainfall and inflow to the lake occurs from December to April. The chaparral vegetation of the drainage produces little humus, thus limiting the amount of iron-chelating humic and fulvic acids in the inflow. Sediment-rich river water provides a high phosphorus-loading rate of 142 $mg \cdot m^{-3} \cdot yr^{-1}$ (derived from Horne and Goldman 1972). Alkalinity in Clear Lake varies from 90 to 170 mg $CaCO_3 \cdot L^{-1}$ and pH during our experiments was above 8.0 (Table 1). The lake has an area of 170 km^2 and is divided into three basins, all shallow with mean depths ranging from 6 to 12 m. The hydraulic residence time of 3 yr is short. The lake is polymictic. Sediment surface anoxia is frequent but often of only a few days duration, and periods of anoxia may occur in different basins at different times. Despite its name, Clear Lake is eutrophic, and Secchi depths are shallow (0.5–3.0 m) as a result of inorganic turbidity and algal blooms which often reach nuisance proportions. Further details of the limnology of the lake can be found in Goldman and Wetzel (1963) and Horne and Goldman (1972).

Field Collections

Measurements of iron, algae, and related physical and chemical parameters were made at 2- to 4-wk intervals during the 1975 algal bloom. Major nutrients and phytoplankton biomass were measured at one station in the pelagic zone of the upper basin. Chemical and algal biomass data were provided by the California Department of Water Resources. Nitrate was measured by the brucine method, ammonia by nesslerization, and soluble reactive phosphorus (SRP) by the stannous chloride method (APHA 1971). Iron depth profiles in the upper basin were made using water collected in an opaque polyvinyl chloride Van Dorn bottle. These samples were collected by overflowing a bottle 2–3 times its volume, stoppering tightly, and then storing in the dark until filtered. Temperature and dissolved oxygen were measured with a temperature–oxygen probe. Most other measurements were made on water pooled from sampling at widely spaced stations in the pelagic zone of each basin (three, four, and five stations in the respective oaks, lower and upper basins). Elder (1977) reported diel variations in dissolved iron and in iron-uptake capacity of the plankton in an arid-zone lake. To test if diel variations in dissolved iron occurred in Clear Lake, we measured surface water concentrations seven times spread over a 30-h period on June 11–12, 1975. Single samples were taken at each time interval and analyzed in duplicate. Additional measurements were made on surface samples taken with polyethylene buckets.

Samples to measure nitrogen fixation rates were collected at the five stations in the upper basin of the lake. Water was collected at six depths through the photic zone with a Van Dorn bottle and pooled with water of equal depths from the other stations. Nitrogen fixation rates were estimated by the acetylene reduction method as described by Horne and Goldman (1972). Fifty millilitres of water was placed in a 62-mL serum bottle, 1 mL of freshly generated acetylene was injected, and the sample was agitated vigorously for 15 s. Samples were incubated in situ for 2 h at the appropriate depths, shaken vigorously, and 0.5 mL of gas withdrawn with a disposable syringe for subsequent gas-chromatographic analysis. Subsequent tests showed that 1 mL of acetylene does not saturate the enzyme system and results in approximately a 50% underestimate of acetylene-reduction rates. Consequently all rates were doubled to correct for this error. Although this procedure may have introduced some error in the estimates of absolute rates of nitrogen fixation, it should have had little effect on our bioassay results because treatments were always compared relative to controls. Chlorophyll *a* was measured spectrophotometrically after pigment extraction in boiling methanol (Talling and Driver 1963).

There is no accepted analytical procedure to determine biologically available iron (cf. Shapiro 1969; Davies 1970; Owens and Chaney 1971; Strickland and Parsons 1972; Anderson and Morel 1980). Consequently, we elected to measure two readably definable fractions: total iron and total dissolved iron. Dissolved iron was determined on water passing through glass fiber (GFC) and Ha millipore (0.45 μm) filters previously washed with 5–10 mL of 0.1 $mol \cdot L^{-1}$ HCl and rinsed with redistilled water. The terminology "dissolved" must be interpreted guardedly as Koenings (1976) has shown that up to 85% of this iron fraction may exist as colloids. Iron concentrations were measured colorimetrically in a 10-cm cell using a modified ferrozine method (Stookey

TABLE 1. Summary of culture conditions for each of the bioassay experiments. The growth of the control cultures in each experiment is shown by the mean daily percentage change in chlorophyll *a* during the period of growth or decline. Asterisks indicate nutrient additions made daily. Key: % Het = % Heterocysts; Lab = Laboratory incubations; Lake = in situ tube incubations; Aph = *Aphanizomenon flos-aquae*; Ana = *Anabaena sp.*; Dia = miscellaneous diatoms; Grn = miscellaneous green algae; Mel = *Melosira sp.*; T = trace. Nitrogen fixation rates are in units of μmol $C_2H_4 \cdot L^{-1} \cdot h^{-1}$. Volumes of dominant algae are in mm^3/L.

			Initial sample characteristics					Control		Nutrients added (μg/L)		
Exp. No.	Dates	Type	pH	Dominant algae Type	(vol)	% Het	Chl.*a* (μg/L)	Growth (%/d)	Max N fixation	Fe	PO_4-P	NO_3-N
1	Feb. 25–March 4 1975	Lab	8.3	Aph	22	0.1	70	10	220	50	100	200
				Ana	T							
2	March 13–March 19 1975	Lab	8.0	Aph	7	T	21	−5	4	50	100	200
				Grn	T							
				Dia	T							
3	April 28–May 7 1975	Lab	8.0	Aph	18	0.2	27	22	380	50	—	200
I	June 25–July 3 1975	Lake	8.2	Aph	21	0.6	25	0	40	20*	—	—
4	June 25–July 4 1975	Lab	8.3	Aph	21	0.6	32	15	300	20*	100	200
II	July 10–July 18 1975	Lake	8.0	Aph	58	1.5	50	−10	380	20*	—	—
5	July 10–July 15 1975	Lab	8.0	Aph	58	1.5	54	−16	66	20*	—	—
6	Sept. 15–Sept. 25 1975	Lab	8.0	Aph	1	~2.5	22	60	10	10*	100	200
				Ana	T							
				Mel	6							
7	Oct. 6–Oct. 16 1975	Lab	8.3	Aph	T		30	30	260	10*	—	200
				Ana	6	1.4						
				Mel	92							
8	May 18–May 26 1976	Lab	8.4	Aph	2	T	20	10	2	50	100	200
				Chl	T							
				Mel	1							
9	June 8–June 16 1976	Lab	8.4	Aph	36	0.5	44	10	180	200*	200	—
				Dia	T							

1970). The primary modifications were to: (1) recrystallize the hydroxylamine hydrochloride (Strickland and Parsons 1972) to minimize blank values and (2) add 50% more acid (and buffer) and to increase the heating period to 30 min to increase digestion of particulate iron. All glassware used in the study was originally soaked in hot 50% HCl for at least 20 min, and rinsed 3–4 times with glass-distilled water.

LABORATORY BIOASSAYS

Nine laboratory bioassays were conducted with water collected in the mornings from the top meter of the pelagic area in the upper basin of Clear Lake. A series of 4-L wide-mouthed Erlenmeyer flasks (Pyrex glass) were each filled with 2 L of unfiltered lake water and stoppered with polyester wool plugs. The flasks were incubated at room temperature under fluorescent light (General Electric Cool White bulbs) at intensities of 950–1250 lx (about 40 μEinst $\cdot m^{-2} \cdot s^{-1}$ with a 2-pi collector) with an 18:6 photoperiod (light:dark). The flasks were swirled gently by hand for several seconds two to three times daily to redistribute the algae. Bioassays lasted from 7 to 10 d (Table 1).

Nutrient additions to the cultures were usually done only at the start of the experiment but in some cases we added iron at daily intervals after subsamples had been collected for metabolic measurements of the algae. Combined additions of Mo, Mn, Cu, or Zn were tested in three bioassays, but these micronutrients did not stimulate algal growth or nitrogen fixation and their results are not included. Additions of Fe, NO_3, NH_4, and PO_4 were made from stock solutions of the respective Analar grade salts of $FeSO_4 \cdot 7H_2O$, KNO_3, NH_4Cl, and KH_2PO_4. Treatments were done in duplicate. Triplicate control flasks received additions of distilled water comparable in volume to those of the treatments. Except as noted, responses of the controls and treatments were compared for statistical differences using Student's *t*-tests.

At 1- or 2-d intervals, duplicate subsamples from each flask were normally taken for measurements of carbon and nitrogen fixation. Single samples were taken for chlorophyll *a* analysis. Carbon fixation was measured using the ^{14}C technique as described by Horne and Goldman (1974). Nitrogen fixation and chlorophyll *a* were measured as described previously. The subsamples were incubated for 2 h under the same light and temperature conditions as the culture flasks. Algae preserved in Lugol's solution were used for subsequent counting. Counting was done in a Sedgwick–Rafter cell and ~9% of the cell volume was counted. Algal volumes were estimated by assuming that the algae conformed in shape to fixed geometric forms.

The movement of added iron from solution into the seston was measured after the addition of 50 μg $\cdot L^{-1}$ $FeSO_4$ to 2-L samples of both unfiltered and filtered (0.45 μm) lake water in 4-L flasks. The samples were incubated as described previously, and after 1–3 min (T_o), 7-h and 28-h duplicate samples were withdrawn from each flask to measure total and dissolved iron.

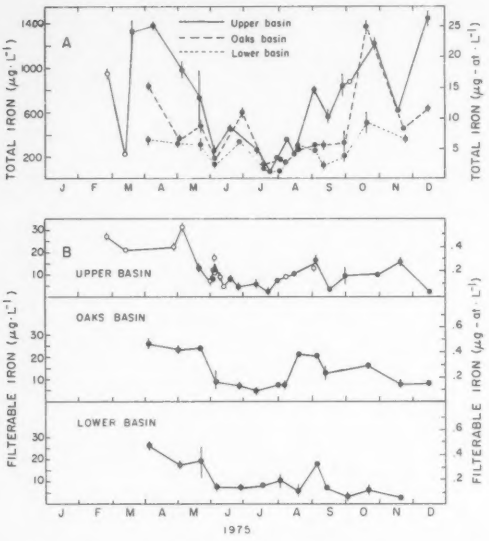

FIG. 1. Concentrations of total iron (A) and 0.45 μm dissolved iron (B) in the pelagic zone of each basin of Clear Lake, California, during 1976. Closed circles represent integrated 0- to 4-m samples and open circles represent surface samples. Error bars show ± 1 SD of the mean of replicate analyses of single field samples.

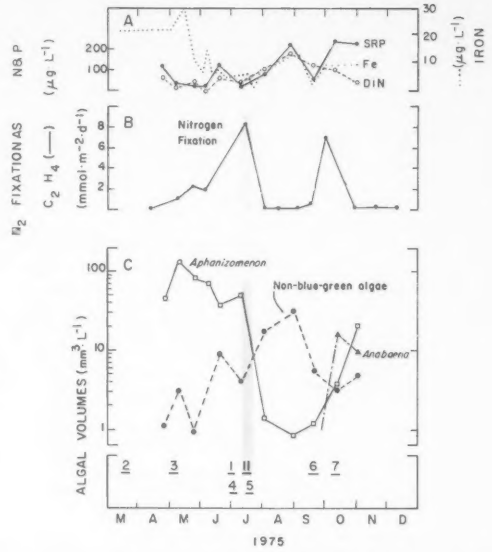

FIG. 2. (A) Concentrations of soluble iron (Fe), soluble reactive phosphorus (SRP), and dissolved inorganic nitrogen (DIN) in the surface waters (0 m) of the upper basin of Clear Lake. (B) Nitrogen fixation (as ethylene produced) in the photic zone (0–4 m). (C) Biovolumes of major algal groups in the upper basin of Clear Lake. The timing and duration of the 1975 bioassay experiments are shown by numbered bars at the base of (C). The timing of the critical field experiment (II) is shown by the shaded vertical bar.

FIELD BIOASSAYS

As confinement of natural waters in small containers may alter the amount of dissolved iron present (McMahon 1969; Lewin and Chen 1973), we performed two in situ experiments in large polyethylene tubes (polytubes) incubated in the pelagic zone of the lake (Goldman 1962). The tubes were made of translucent plastic (100 μm thick) and supported by polyethylene pipe hoops to form 56-cm-diameter cylinders with their tops open to the air. The bottoms were tied closed at 3.2 m (Experiment I) or at 2.0 m (Experiment II), giving respective volumes of 750 and 500 L. Two tubes were chosen at random for controls and two bags received daily additions of 50 μg $Fe \cdot L^{-1}$ as $FeSO_4$ after samples had been collected for physiological measurements. At 1- or 2-d intervals the water in each tube was mixed thoroughly and duplicate samples taken to measure nitrogen and carbon fixation rates and chlorophyll *a* concentrations. Carbon and nitrogen fixation samples were incubated in the lake at 1.0 m (Experiment I) or 1.5 m (Experiment II), the respective Secchi depths at the start of each experiment. At the start of each field bioassay a water sample was collected from the same site for use in concurrent laboratory experiments.

During Experiment II, oxygen and temperature profiles in the polytubes and in the lake were taken on several occasions with an oxygen–temperature probe at 12:00. Samples taken after the polytubes were mixed were used to analyze for pH and dissolved inorganic carbon (infrared carbon analyzer). Temperatures in the tubes and the lake were nearly identical and dissolved oxygen, dissolved inorganic carbon, and pH in the tubes never differed more than 10% from lake conditions. Midday dissolved oxygen concentrations in the polytubes and in the lake were above saturation throughout the experiment, reflecting the bloom conditions of the algae at that time. On the 8th day of Experiment II, one of the polytubes was badly damaged and measurements in it discontinued.

Results

LAKE CYCLES

Total iron concentrations in Clear Lake varied seasonally from a low of 65 μg $\cdot L^{-1}$ (1.2 μg-at $\cdot L^{-1}$) in August to over 1300 μg $\cdot L^{-1}$ (21.8 μg-at $\cdot L^{-1}$) in the winter months (Fig. 1A). In the spring, total iron concentrations were highest in the upper basin, but by June, concentrations in all three basins had declined to similar levels. Multiple linear regression indicated that of the parameters measured, total iron concentrations were most closely correlated with turbidity measurements ($r = 0.86$; $P < 0.01$). Turbidity in Clear Lake is usually not positively correlated with chlorophyll *a* as most algae are in large colonies. Consequently, addition of chlorophyll *a* concentrations to the multiple linear regression with turbidity alone did not significantly improve the correlation [$P = 0.25$; $F = 0.48$ (1,34 df)]. This suggests that total iron concentrations were not affected seasonally by algal concentrations or that the relationship was masked by other factors. Most of the iron in the water column is probably associated with inorganic particulate matter, some of which enters the

lake during winter runoff, and some of which is resuspended from the lake bottom by winds.

Dissolved iron in Clear Lake was low throughout the year, and all three basins had similar levels (Fig. 1B). Between 0.1 and 8.8% of the total iron was found in the dissolved fraction. Maximum values of 30 $\mu g \cdot L^{-1}$ of dissolved iron were found in the early spring, but by June concentrations had decreased to 5–7 $\mu g \cdot L^{-1}$ (0.1 $\mu g\text{-at} \cdot L^{-1}$). In July, a low level of 2 μg Fe$\cdot L^{-1}$ (0.04 $\mu g\text{-at} \cdot L^{-1}$) was recorded in the upper basin. After July, the seasonal pattern of dissolved iron became very irregular, with concentrations fluctuating between 5 and 20 $\mu g \cdot L^{-1}$ in each basin. The decline in May of dissolved iron in the upper basin occurred during the spring *Aphanizomenon flos-aquae* bloom (Fig. 2). However, multiple regression analysis indicated that dissolved iron was not significantly correlated with either the biological or physical factors which we measured throughout the year (nitrogen fixation, chlorophyll *a*, pH, bottom temperature, turbidity). Algal biomass samples were collected on different dates than were the other parameters and could not be included in the multiple regression analysis.

Dissolved iron concentrations varied little during the diel cycle measured, with a mean concentration of 4.4 + 1.0 $\mu g \cdot L^{-1}$ (mean + SD). The only significant deviation was a 50% decrease in iron to 2.5 + 0.6 $\mu g \cdot L^{-1}$ at 15:00 on the 1st day of sampling. However, this decrease did not occur the following day. The patchiness of water masses within the lake may account for the observed variation.

Iron depth profiles varied considerably between sampling dates. In June, during the spring *Aphanizomenon* bloom, dissolved iron concentrations were maximal at the thermocline (Fig. 3A). Because oxygen concentrations there were high, little soluble iron was expected (Stumm and Lee 1960). The maxima may have been associated with chelators excreted from the algae. We did not sample algae when the profile was made, but samples taken 1 wk before and after, indicated that blue-green algal concentrations (*Aphanizomenon* and *Oscillatoria*) were maximal at the thermocline (3 m). Wholer and Hartman (1973) also found trace metal maxima associated with *Oscillatoria* concentrations at the thermocline. When the July and August samples were taken, the lake was not strongly stratified, few blue-green algae were present, and dissolved iron concentrations increased with depth (Fig. 3B, C). Dissolved iron concentrations were highest in samples taken near the anoxic sediments. These samples may have included some sediment interstitial water due to the disruption of the water–sediment interface by the sampling bottle.

BIOASSAYS

Nitrogen fixation rates of the blue-green algae were markedly and consistently stimulated by additions of iron to Clear Lake water (Fig. 4–7). We have included here the detailed results of only three bioassays, with results from all 11 experiments summarized in Fig. 7 and 8. Detailed results of the other bioassays can be obtained from the authors. Iron

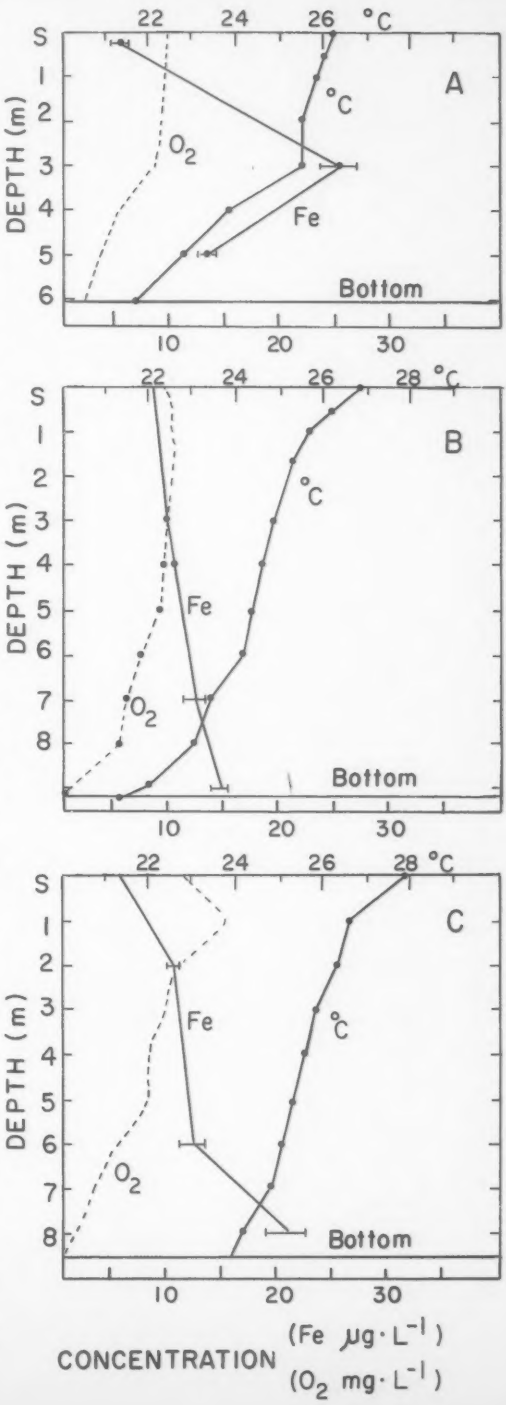

FIG. 3. Depth profiles of dissolved iron, dissolved oxygen, and temperature in the upper basin of Clear Lake. Samples were collected at ~12:00 on each date. Horizontal bars represent standard deviations of replicate assays for iron. (A) June 12, 1975. (B) July 22, 1975. (C) August 10, 1975.

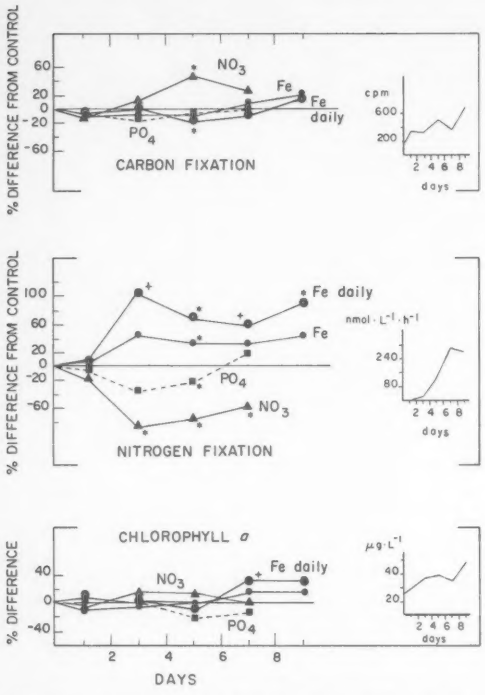

FIG. 4. Experiment 4: effects of nutrient additions on algae during the decline of the spring *Aphanizomenon* bloom (June 25–July 4, 1975). Results are plotted as % difference from controls except in the small inserted graphs which indicate absolute changes in the control cultures. Significance (Student's *t*-test): + ($P < 0.10$); * ($P < 0.05$).

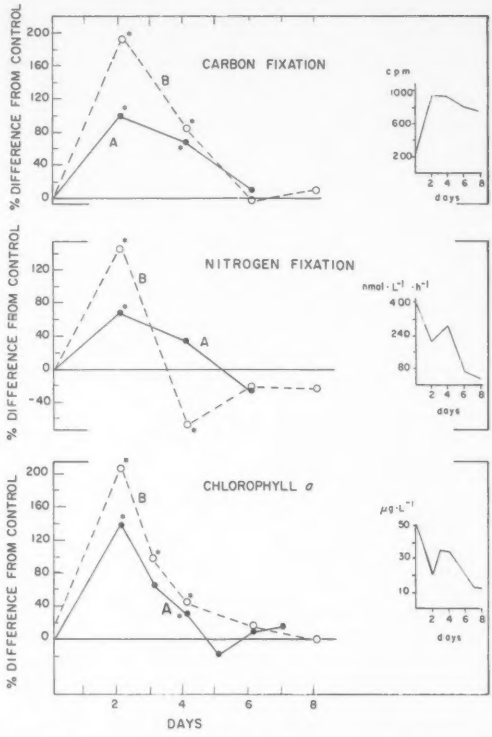

FIG. 5. Experiment II: effects of iron additions (20 $\mu g \cdot L^{-1} \cdot d^{-1}$ on in situ cultures of phytoplankton during the collapse of the spring *Aphanizomenon* bloom in Clear Lake in July, 1975. Responses of the two replicate iron treatments (A, B) are shown separately. Asterisks indicate responses which were outside of the 90% confidence intervals of the duplicated control cultures. Inserts show absolute changes in the control cultures.

stimulation generally was greatest when nitrogen fixation rates were high (Fig. 7, Table 1), indicating a high iron demand for this process. Daily rates of nitrogen fixation were normally stimulated 20–100% above controls by iron additions of 20–50 $\mu g \cdot L^{-1}$, but when 200 $\mu g \cdot L^{-1} \cdot d^{-1}$ was added, stimulation reached 500% above controls (Fig. 6). Iron usually stimulated nitrogen fixation rapidly, significant increases occurring within 2–4 d (Fig. 4–6). Heterocyst frequencies of blue-green algae in iron-treated cultures were normally above control values (Fig. 8B), although these differences were often not significant because of the large variability between replicate counts. However, the consistency of the heterocyst stimulation suggests the iron was important in promoting the differentiation of cells for nitrogen fixation.

In contrast to iron, addition of nitrate markedly suppressed increases in nitrogen fixation and heterocyst frequencies relative to controls (Fig. 4, 6–8). Addition of NH_4 (100 μg $N \cdot L^{-1}$) in Experiment I inhibited nitrogen fixation and heterocyst formation even more than nitrate.

Phosphate additions stimulated heterocyst frequencies above control values in three of the four experiments where *Aphanizomenon* densities were sufficiently high to give reliable counts (Fig. 8). However, these increases were generally not accompanied by stimulation of nitrogen fixation (Fig. 4, 6, 7). In nearly all cases where parallel assays were performed, iron was more stimulatory to nitrogen fixation than phosphorus (Fig. 7).

Iron also significantly stimulated carbon fixation (Fig. 5–7), not only in cultures dominated by *Aphanizomenon* (Experiments I, II, 8, 9), but also when diatoms were abundant (Experiments 6, 7). However, in six of the seven parallel assays, carbon fixation was stimulated more by nitrate than by iron (Fig. 7). Phosphate additions produced variable results, significantly stimulating carbon fixation in two experiments, but giving slight (but insignificant) depression in four other experiments.

In most experiments, both final algal volumes and chlorophyll *a* were stimulated by nitrate or iron, but usually to a lesser degree than the stimulation of carbon or nitrogen fixation (Fig. 4–7). Chlorophyll *a* levels and final algal

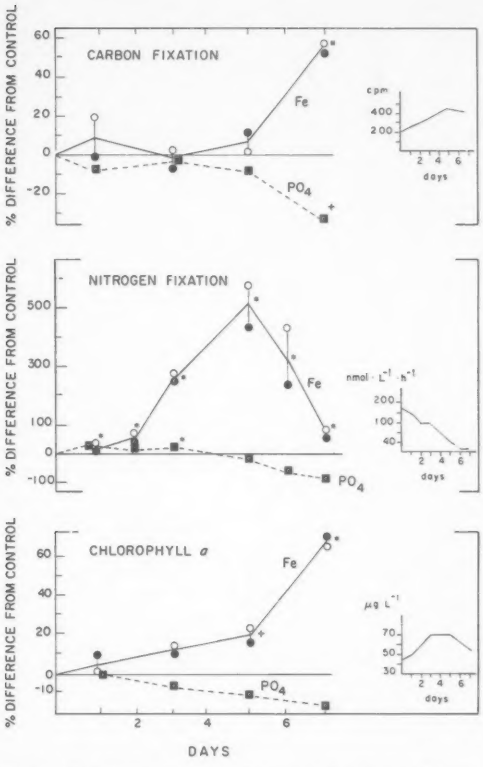

FIG. 6. Experiment 9: effects of iron and phosphate additions on algae during the spring *Aphanizomenon* bloom in June, 1976. Results plotted as in Fig. 4. Note differences in the ranges of ordinates in the three figures. The mean response of cultures receiving $FeSO_4$ (○) or $FeCl_2$ (●) are plotted, as there were no significant differences between the two treatments.

volumes in phosphorus treatments were usually below control levels, but significant stimulation of chlorophyll occurred in one experiment.

Laboratory and field algal cultures responded differently in the two comparative experiments. In the first comparison made 2–4 wk before the collapse of the spring *Aphanizomenon* bloom (Fig. 2), growth was vigorous and nitrogen fixation rates high in the laboratory cultures (Experiment 4), but not in the field cultures (Experiment 1; Table 1). Results from the actively growing laboratory cultures indicated that iron and nitrogen were limiting algal nitrogen fixation and photosynthesis (Fig. 4), whereas in the field cultures, iron additions did not stimulate the algae (Fig. 7).

Field and laboratory bioassays (Expt. II and 5, respectively) were also done during the final collapse of the spring *Aphanizomenon* bloom. These experiments also coincided with the peak of *Aphanizomenon*-related nitrogen fixation in the lake (Fig. 2), indicating that combined nitrogen in the lake was inadequate to meet algal demand at this time. In the

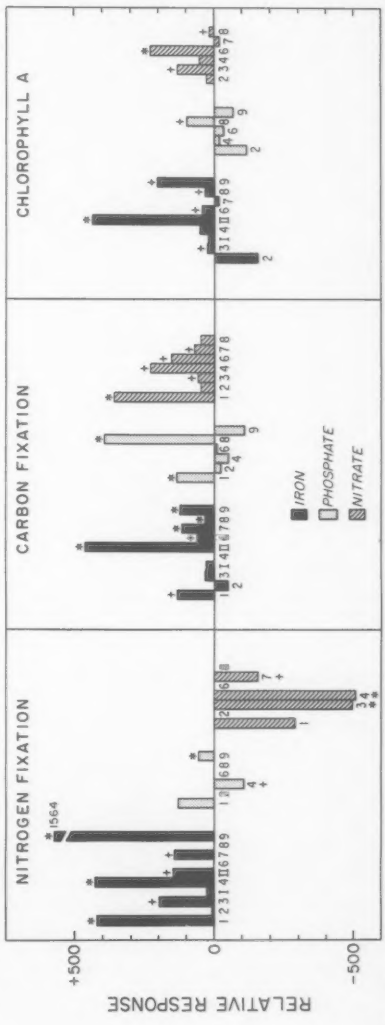

FIG. 7. Summary of the effects of iron, nitrate, and phosphate on nitrogen fixation, carbon fixation, and chlorophyll *a* in the nutrient bioassays. The numbers at the base of each bar are the bioassay experiment numbers. The relative response was calculated by integrating the area under the time — % difference from control plots (0–8 d) during the period of stimulation or depression. Initial lags or a depression following a large stimulation were not included in the integration. For example, an initial stimulation of 20% for 5 d, followed by below control levels for 3 d, would give a relative response of 100 (%·d). Experiments with significant ($P < 0.05$) stimulation on one (+) or more (*) days are indicated. As nutrient concentrations and the initial states of the inocula varied between bioassays, all of the experiments are not directly comparable. Table 1 summarizes the experimental conditions of each bioassay. Chlorophyll was not analyzed in Experiment 1, and the results of Experiment 5 are not shown because algae in both controls and treatments suffered rapid die-offs.

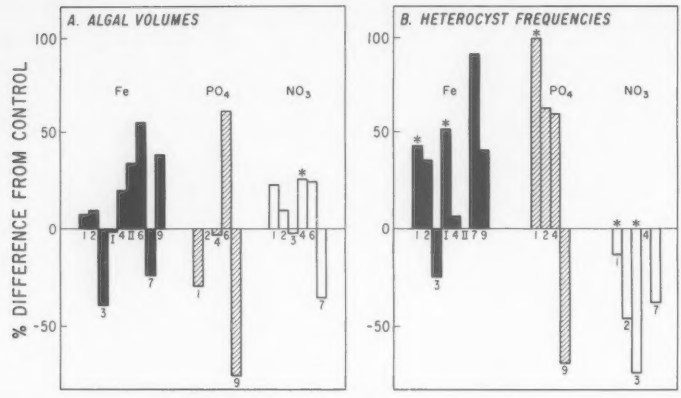

FIG. 8. (A) Effects of iron, nitrate, and phosphate additions on the final volume of the dominate algal species in the bioassay experiments (see Table 1 for species). (B) Final heterocyst frequencies of *Aphanizomenon* or *Anabaena* in the nutrient bioassays. Numbers at bases of histograms refer to experiment numbers. Values significantly different from controls [$P < 0.05$; Dunnet test (Zar 1974)] are indicated with asterisks. Statistical analyses were not possible for experiments II and 7 because of missing samples.

laboratory cultures, algae in both control and iron treatments suffered rapid die-offs: within 3 d, chlorophyll levels had declined 80% below initial levels, nitrogen fixation rates fell to zero, and *Aphanizomenon* volumes declined from 58 to 2 $mm^3 \cdot L^{-1}$. In the control field cultures, chlorophyll concentrations and nitrogen fixation rates also declined rapidly (Fig. 5 insets), and *Aphanizomenon* volumes declined by 50%, thus mimicking the lake populations and the laboratory cultures. Changes in carbon fixation rates cannot be compared, as a result of variable light regimes produced by intermittent cloudiness during the experiment.

In contrast to the control cultures in the field and laboratory, algae in the polytubes receiving iron grew well and maintained high nitrogen fixation rates, prolonging bloom conditions for an additional 2–5 d (Fig. 5). After the initial stimulation, nitrogen fixation rates in each of the two replicate iron treatments responded differently. In one treatment (A), fixation rates remained above controls through the 4th day of the experiment, whereas in the replicate treatment (B), fixation declined below controls on day 4. This difference may have been due to polytube B inadvertently receiving its iron addition 6 h later than polytube A on the 3rd day of treatment.

Stimulation of algal metabolism was enhanced by making iron more available to the algae. Nitrogen fixation rates of *Aphanizomenon* cultures which received daily additions of iron (20 $\mu g \cdot L^{-1}$) was about 100% greater than cultures which received only an initial addition of 50 $\mu g\ Fe \cdot L^{-1}$ (Fig. 4). Addition of a chelator also increased algal response. When iron was added with EDTA (5 $\mu mol \cdot L^{-1}$) in Experiment 8, iron stimulation of carbon fixation was significantly enhanced:

Addition:	Control	EDTA	$FeCl_2$	EDTA + $FeCl_2$
Relative fixation:	100	116	118	131

(Results not significantly different are underlined: $P < 0.05$; Newman–Keuls test (Zar 1974)). However, because EDTA alone significantly stimulated fixation, we cannot rule out the possibility that EDTA detoxified some component in the water (Jackson and Morgan 1978) rather than increasing iron availability. Finally, when iron was added at the high rate of 200 $\mu g \cdot L^{-1} \cdot d^{-1}$ (as either $FeCl_2$ or $FeSO_4$), much greater stimulation of nitrogen fixation was produced than in experiments where 20 or 50 $\mu g\ Fe \cdot L^{-1}$ was added (Fig. 6, 7).

Iron disappeared rapidly from solution when added to lake water with plankton, but remained in solution for several hours when added to filtered lake water (Fig. 9). In lake water, 90% of the dissolved iron was removed from solution within 1–3 min (the time to filter the samples) and decreased to control levels within 7 h. Total iron concentration remained relatively stable, indicating that the dissolved iron moved into the particulate phase and was not adsorbed to the container walls (Fig. 9A). In filtered lake water, 20% of the added iron was still detectable in the dissolved fraction after 7 h, but declined to control levels within 28 h (Fig. 9B). The rapid movement of iron into the particulate phase in the unfiltered water, but not in the filtered water, could be due to either algal uptake or to rapid precipitation in the presence of seed particles. However, in similarly conducted experiments, Elder (1977) found that there were diel cycles of iron "uptake" and that "uptake" was mediated by the prior light history of the lake water, thus suggesting that phytoplankton can rapidly remove added iron from solution.

Discussion

The field and bioassay results both support the hypothesis that iron limits algal growth, and particularly nitrogen fixation, in Clear Lake. Dissolved and total iron levels declined in the lake during the *Aphanizomenon* bloom and reached their lowest levels during the period of bloom collapse (Fig. 2). In the nine laboratory bioassays, iron significantly stimulated nitrogen fixation five times and carbon fixation six

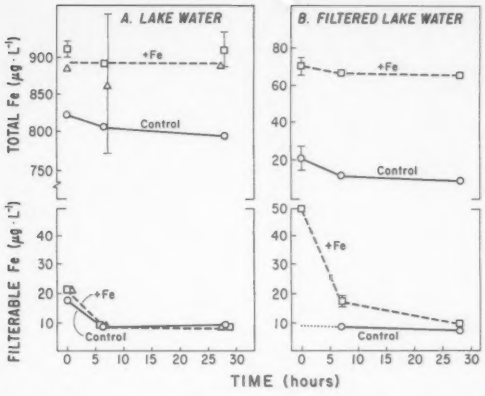

FIG. 9. Changes in dissolved iron following the addition of 50 μg $FeSO_4 \cdot L^{-1}$ to Clear Lake water (Dec. 3, 1975). (A) Fate of iron added to unfiltered lake water with 32 μg·L^{-1} chlorophyll *a*: (△, □) duplicate iron treatments; (○) control. (B) Fate of iron added to 0.45-μm membrane-filtered lake water. Each point represents the mean of duplicate Fe determinations with the range shown if it extends beyond the symbols.

times (Fig. 7). However, laboratory assays may produce artifacts. The moderate and sustained irradiance levels in the laboratory may stimulate growth rates of the algae, thus increasing demands for nutrients above those in the lake. This may explain the difference between Experiment 4 (laboratory assay) where algal growth was rapid and iron stimulated nitrogen fixation, and the concurrent field bioassay (I), where nitrogen fixation and growth rates were low and there was no stimulation by iron (Table 1; Fig. 7). In vitro assays could also modify nutrient recycling from zooplankton, hypolimnetic water, and the sediments. Although zooplankton will effect recycling rates of nitrogen and phosphorus, preliminary experiments indicate they do not excrete iron (W. Wurtsbaugh unpublished data). Irradiance levels used in laboratory experiments could also reduce natural rates of photochemical cycling of iron, thus making it less available (Anderson and Morel 1982). Consequently, one can question if our laboratory bioassays adequately represent results which would occur in Clear Lake.

The results of Experiment II, a field bioassay conducted during the collapse of the *Aphanizomenon* bloom, suggest that the laboratory experiments are indicative of the importance of iron for natural lake populations. Algae in control cultures in this experiment declined rapidly (Fig. 5 insets), following the decline of *Aphanizomenon* which was occuring in the lake. A small daily dosage of 20 μg·L^{-1} of iron maintained the algal populations at high levels for several additional days before they too declined (Fig. 5). We do not know if the algae eventually exhausted some other nutrient or whether the small amount of added iron was insufficient to meet demands of the high algal biomass (about 65 μg chlorophyll $a \cdot L^{-1}$). Eyster (1970) found that when iron ($FeSO_4$) was added as an unchelated salt, concentrations in excess of 10 000 μg·L^{-1} were necessary to support maximum growth of *Nostoc muscorum* during nitrogen fixation. Total iron concentrations in Clear Lake at the time of the collapse were below 400 μg·L^{-1} and dissolved iron was at its lowest level (Fig. 2).

Lange (1974a) has shown that blue-green algae (*Microcystis*) grown to senescence without iron can be killed by exposure to sunlight for 3 h. Dramatic die-offs of *Aphanizomenon* are often observed in Clear Lake and light-induced death has been suggested as the causal force (Horne and Wrigley 1975; Horne unpublished data). The synergistic effect of poor iron nutrition and high light levels may be responsible for these massive declines of *Aphanizomenon* in Clear Lake.

Phosphate additions occasionally stimulated carbon fixation, but more frequently had no effect on algal growth. It is interesting that phosphate usually stimulated heterocyst formation more than did iron (Fig. 8) but usually without a concomitant increase in nitrogen fixation rates (Fig. 7). This suggests that both P and Fe could act together to limit nitrogen fixation. In Experiment 4, we tested this, but found that PO_4 additions to iron-treated cultures provided no additional stimulation of nitrogen fixation. Because phosphorus may stimulate heterocyst formation without increasing nitrogen fixation, caution in the use of heterocyst counts as an indirect measure of fixation is suggested. Phosphate limitation of nitrogen fixation has been indicated in other lakes (Stewart et al. 1970; Vanderhoef et al. 1972). However, care should be exercised in correlating rates of nitrogen fixation with environmental phosphate concentrations as phosphate and iron are often positively correlated in natural waters (Hutchinson 1957).

Investigations using bioassay techniques have found iron to be limiting to algal productivity in a variety of aquatic systems (Menzel and Ryther 1961; Schelske et al. 1962; Tranter and Newell 1963; Wetzel 1966; Sakamoto 1971; Likens 1972; Goldman 1972; Elder and Horne 1977; Lin and Schelske 1981; Priscu et al. 1982). Lean and Pick (1981), citing the work of Murphy et al. (1976), question these results. They suggest that iron limitation is induced by blue-green algae which release chelating substances (siderochromes) that make iron unavailable to other species. Thus they suggest that it is "hoarding," not absolute lack of iron, that limits algal growth in these systems. Three factors lead us to doubt this hypothesis: (1) Our results, and those of Elder and Horne (1977) indicate actual stimulation of blue-green algae by iron additions. If blue-green algae were simply hoarding iron, this stimulation would not have occurred. (2) The results of Morton and Lee (1974) indicate that adding iron to mixed-species cultures causes a shift in algal composition from communities dominated by green algae to ones dominated by blue-green algae. A change in the reverse direction would be expected if Lean and Pick's hypothesis is correct. (3) Siderochromes have only been shown to be produced by growing blue-green algae at extremely low iron concentrations (Simpson and Neilands 1976). These factors support the previous suggestions of Murphy et al. (1976) and Lean et al. (1978) that the production of siderochromes is a response to iron-limiting conditions and that these chelators are important in determining the outcome of interspecific competition.

Algal productivity in Clear Lake is most often directly limited by combined nitrogen (NO_3, NH_4), but occasionally

by iron or phosphorus. However, low iron levels aggravate the effects of low nitrogen by limiting nitrogen fixation, and thus the growth of blue-green algae. Because blue-green algal nitrogen fixation provides over 40% of the nitrogen in the annual nutrient budget of Clear Lake, this fixation is important to other algal groups as well (Horne and Goldman 1972). Thus, limitation of nitrogen fixation by iron or other micronutrients can be important in aquatic systems and sheds doubt on the hypothesis that algal productivity will always be limited by phosphorus.

Acknowledgments

S. Vasak and C. Carmiggelt assisted in various aspects of the study and J. Elder, T. Murphy, D. Paolini, W. Davison, and T. Abresh critically reviewed earlier versions of the manuscript. This work was supported by the Clear Lake Flood Control and Water Conservation District and the California Department of Water Resources.

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Validation of Age Estimation in the Harp Seal, *Phoca groenlandica*, Using Dentinal Annuli

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We investigated the validity and accuracy of age estimation in harp seals, *Phoca groenlandica*, using a sample of 155 known-age teeth from seals age 3 mo to 10 yr. Under transmitted light, transverse sections of harp seal canine teeth showed distinct incremental growth layers (IGLs) in the dentine. The first growth-layer group (GLG), representing 1st-year growth, consists of two IGLs: an outer layer of opaque dentine, bounded by the neonatal line, and an inner layer of translucent dentine. Subsequent GLGs, each representing 1 yr of growth, generally consist of three IGLs: an outer layer of interglobular dentine deposited during the annual molt in April, a middle layer of opaque dentine formed during the northward spring migration (May–June), and an inner layer of translucent dentine formed from July to March. We show that dentinal GLGs can be used to estimate the absolute age of harp seals. The accuracy of the method decreases with age. Only 72.4% of estimates of 0-group seals were correct using only transverse sections. These errors were virtually eliminated (99.0% correct age determination) when the tooth root was examined. Based on a single examination of a transverse section, the probabilities of correctly estimating age are 0.983, 0.889, 0.817, and 0.553 at ages 1, 2, 3, and 4+ yr, respectively, when clearly inaccurate tag-tooth associations are omitted. The respective probabilities are only slightly higher when age is based on the average of five blind readings, being 1.0, 0.889, 0.833, and 0.625. Beyond age 3 yr, existing data are insufficient to estimate reliably the accuracy of age determined by counting GLGs.

BOWEN, W. D., D. E. SERGEANT, AND T. ØRITSLAND. 1983. Validation of age estimation in the harp seal, *Phoca groenlandica*, using dentinal annuli. Can. J. Fish. Aquat. Sci. 40: 1430–1441.

Le présent rapport porte sur l'étude de la validité et de la précision de la méthode de détermination de l'âge des phoques du Groenland, *Phoca groenlandica*, à l'aide d'un échantillon de 155 dents prélevées de phoques âgés de 3 mois à 10 ans. L'examen de coupes transversales de canines a révélé la présence de couches distinctes de croissance (CC) dans la dentine. Le premier groupe de couches de croissance (GCC), qui représente la croissance de la première année, se compose de deux CC, soit une couche externe de dentine opaque limitée par la ligne néo-natale et une couche interne de dentine translucide. Les GCC suivants, dont chacun représente une année de croissance, se composent généralement de trois CC: une couche externe de dentine interglobulaire déposée pendant la mue annuelle, en avril, une couche mitoyenne de dentine opaque formée pendant la migration vers le nord, au printemps (mai et juin), et une couche interne de dentine translucide formée de juillet à mars. Les auteurs démontrent que les GCC peuvent être utilisés pour évaluer l'âge absolu des phoques du Groenland. La précision de la méthode diminue en fonction de l'âge. Pour le groupe d'âge 0, seulement 72,4 % des estimations au moyen des coupes transversales étaient correctes. Ces erreurs ont été presque complètement éliminées (précision s'élevant à 99,0 %) avec l'examen de la racine de la dent. Les probabilités d'estimation correcte de l'âge s'élèvent

Printed in Canada (J7177)
Imprimé au Canada (J7177)

à 0,983, 0,889, 0,817 et 0,553 pour les âges 1, 2, 3 et 4+ respectivement quand on examine seulement une coupe transversale et qu'on omet les données clairement inexactes sur les dents et l'étiquette. Les probabilités respectives ne sont qu'un peu plus élevées quand l'âge est basé sur la moyenne de cinq lectures par un tiers, soit 1,0, 0,889, 0,833 et 0,625. Après 3 ans, les données actuelles ne permettent pas d'évaluer sûrement la précision de l'âge déterminé par le dénombrement des GCC.

Received December 17, 1982
Accepted May 30, 1983

Reçu le 17 décembre 1982
Accepté le 30 mai 1983

THE ability to determine accurately the age of an animal is essential to the study of population dynamics. Incremental growth of cementum, dentine, and bone has been used for age determination in many species of mammals (Klevezal and Kleinenberg 1967; Jonsgard 1969; Morris 1972; Spinage 1973; Grue and Jensen 1979; Scheffer and Myrick 1980), including over 20 species of pinnipeds (Laws 1962). The technique is based on the assumption that such tissues are deposited in a cyclic manner, producing histologically distinct and permanent layers that can be related to the actual age of an animal. As there is no resorption of calcium from teeth (Johansen 1967; Scott and Symons 1974), the structure and appearance of the dental tissues should accurately reflect the history of growth of an individual.

Incremental growth layers in the teeth of marine mammals were described or illustrated by zoologists as early as 1840 (Owen 1840–1845; Scheffer and Myrick 1980). However, it was not until about 1950 that the value of dental layers for determining the age of marine mammals was generally recognized (Scheffer 1950; Laws 1952, 1953; Nishiwaki and Yagi 1953). Laws (1962) reviewed methods of age determination in seals with special reference to dental growth layers.

Several methods have been proposed to determine the age of harp seals, *Phoca groenlandica*. Plekhanov (1933) found transverse growth ridges in the claws of harp seals which enabled him to estimate the age of animals up to 13 yr. He was working with specimens of unknown age, however, and was unable to check his conclusions. Chapskii (1952) used the number of layers in the periosteal zone of the lower jaw to estimate the age of harp seals.

The method of age determination in harp seals using dentinal annuli was first described in detail by Fisher (1954). He examined about 3000 canine teeth, half taken from seals on the southward migration in January, and the remainder from whelping and molting concentrations in March and April, respectively. Based on this material he deduced the annual pattern of dentine layering and its value in estimating age.

Although incremental dental growth layers have been widely used to determine the age of many mammals, validation of the method using known-age animals has been possible in only a limited number of species. Among pinnipeds, the teeth of a number of known-age animals have been examined in the northern fur seal, *Callorhinus ursinus* (Scheffer 1950; Anas 1970); Cape fur seal, *Arctocephalus pusillus* (Fletemeyer 1978); grey seal, *Halichoerus grypus* (Hewer 1964; A. W. Mansfield, Arctic Biological Station, Ste. Anne de Bellevue, Que., personal communication); southern elephant seal, *Mirounga leonina* (Carrick and Ingham 1962); and hooded seal, *Cystophora cristata* (Øritsland unpublished data).

Harp seals are commercially important (Sergeant 1976) and a method of accurate age determination is important in understanding the influence of the harvest on the dynamics of the population. In this study, we use a sample of 155 known-age specimens to investigate the validity and accuracy of age estimation in harp seals based on dentinal annuli.

Materials and Methods

The canine teeth of 155 known-age harp seals from 0 to 10 yr of age were studied (Table 1). All animals were tagged or branded within 2 wk of birth making it possible to determine age to the nearest month. For convenience in determining known age, a birth date of March 1 was assumed. This introduces little error, as harp seals in the White Sea give birth in late Feburary and early March, in the northwest Atlantic population a few days later, and in the Jan Mayen population in late March (Sergeant 1976). About 92% of the material comes from the northwest Atlantic population (Table 1).

Lower jaws were boiled in water for ~1 h to facilitate extraction of canine teeth. Transverse sections of teeth were cut just below the enamel cap (Fig. 1, zone A) at 200–250 μm. Sagittal sections were also prepared to illustrate the internal gross anatomy of the dentine and, in particular, to illustrate the position of the neonatal line. Ages were estimated from transverse sections only because incremental growth lines were difficult to differentiate and interpret in most sagittal sections. Teeth and thin sections were stored in a solution of equal parts of water, 70% ethanol, and glycerine.

All sections were examined with transmitted polarized light using a 6× to 50× binocular microscope. Generally, thin sections were placed in a petri dish containing a small quantity of water to prevent desiccation of the sample, as dry sections become opaque making examination difficult and unreliable. A small number of transverse sections were mounted on glass slides with Permount. In general this method of storage proved unsatisfactory, because the specimens tended to become opaque.

All measurements of dentine thickness were made with an ocular micrometer. The width of the pulp canal and total length of the tooth were measured with calipers. The standard error is given with mean values unless otherwise stated.

There is considerable variation in the terminology used to describe incremental growth layers in dentine and cementum. To avoid confusion, we have adopted the usage proposed by the International Conference on Determining Age of Odontocete Cetaceans (Perrin and Myrick 1980). Incremental growth layers (IGLs) are distinct layers parallel with the formative surface of dentine which contrast with adjacent layers based on their optical density under transmitted light. Growth

TABLE 1. Origin of known-age harp seal teeth examined.

Location marked[a]	Sex[b]	Age (yr) at recapture											Total	Area total
		0	1	2	3	4	5	6	7	8	9	10		
Northwest Atlantic														
Gulf of St. Lawrence	M		4	4	1		1	2		1		1	14	
	F		2	2		1		1					6	87
	Unk	15	23	14	5	1	6	1	1	1			67	
Front	M	4	4	1	2				1				12	
	F	6	5		2		1						14	55
	Unk	12	6	11									29	
Jan Mayen	M													
	F													9
	Unk			4	4	1							9	
White Sea	M		1	1									2	
	F		2										2	4
	Unk													
Total		37	47	37	14	3	8	4	2	2		1		155

[a]Front = northeastern Newfoundland and southern Labrador.
[b]M = male, F = female, Unk = unknown.

layer groups (GLGs) are groups of incremental growth layers which may be recognized by virtue of a cyclic repetition. Such a cyclic repetition of GLGs must involve at least one change between translucent and opaque layers.

Results

General Morphology and Anatomy of Canine Teeth

In some phocids, the milk dentition is reabsorbed in utero and the teeth which erupt after birth constitute the permanent dentition (Bertram 1940). In harp seals, the lower canine teeth erupt within 1 wk of birth and at that time consist of an enamel crown below which is found a short thin-walled cylinder of fetal dentine. The average length of the canine at birth is 15.3 ± 0.53 mm (n = 9) and the average diameter of the pulp canal (Fig. 1) is 6.6 ± 0.6 mm. As in other phocids the canine teeth of harp seals grow rapidly, reaching an average length of 26.1 ± 0.84 mm (n = 11) at about 1 yr of age and 93% of this value by 6 mo of age. The diameter of the pulp canal decreases rapidly over the first 12 mo and, except for a small opening for blood vessels and nerves, is closed by cementum in about 3 yr (Fig. 2), although the pulp cavity itself remains large.

Transverse sections of harp seal canines are oval or broadly elliptical in shape. Measurements of dentine thickness, taken along the major axis of these sections, revealed asymmetrical growth. The mean thickness of dentine was significantly greater (paired t, df 80, $P < 0.001$) along the major axis at the buccal side (991 μm; n = 123) of the section (as the tooth is positioned in jaw) than at the labial side (897 μm). In all subsequent analyses, measurements of dentine represent an average of two measurements, one taken from each side of the tooth along the major axis.

Three different types of tissues are seen in sagittal sections of harp seal canines: enamel, cementum, and dentine. Enamel is of little use in determining age as its growth ceases shortly after the tooth erupts (Scott and Symons 1974). Incremental growth layers have been described in cementum and dentine of many species and in many cases age determined from the cementum layer is considered more reliable than that based on dentine annuli, particularly for older animals. In harp seals only a thin layer of cementum is deposited throughout the life of the animal. GLGs in the cementum were observed but were generally indistinct and could not be used reliably to estimate age. Further discussion is limited, therefore, to the dentine layer.

Dentine

Transverse sections of harp seal canines, examined with transmitted light, show distinct dentinal IGLs. In 62% of known-age teeth each GLG, excepting the first, consisted of three IGLs: an outer layer of interglobular dentine which is seen to be reticulated, a middle band of dark or opaque dentine, and an inner band of light or translucent dentine (Fig. 3E). In the remainder of known-age specimens, the outer layer of interglobular dentine was absent and each GLG consisted of only two IGLs (Fig. 3G). In all teeth examined, the first GLG, representing the 1st year's growth, consisted of an outer opaque IGL and an inner translucent IGL (Fig. 3A, E). There are no differences between male and female harp seals in the pattern of dentinal GLGs, based on the limited known-age material and a large sample of specimens of unknown age.

In determining age from transverse sections, it is often difficult to define the extent of the 1st year's growth in the dentine. Often there are confusing accessory opaque IGLs in the translucent dentine (Fig. 3E) which could be counted. Because of this, the neonatal line is an important reference

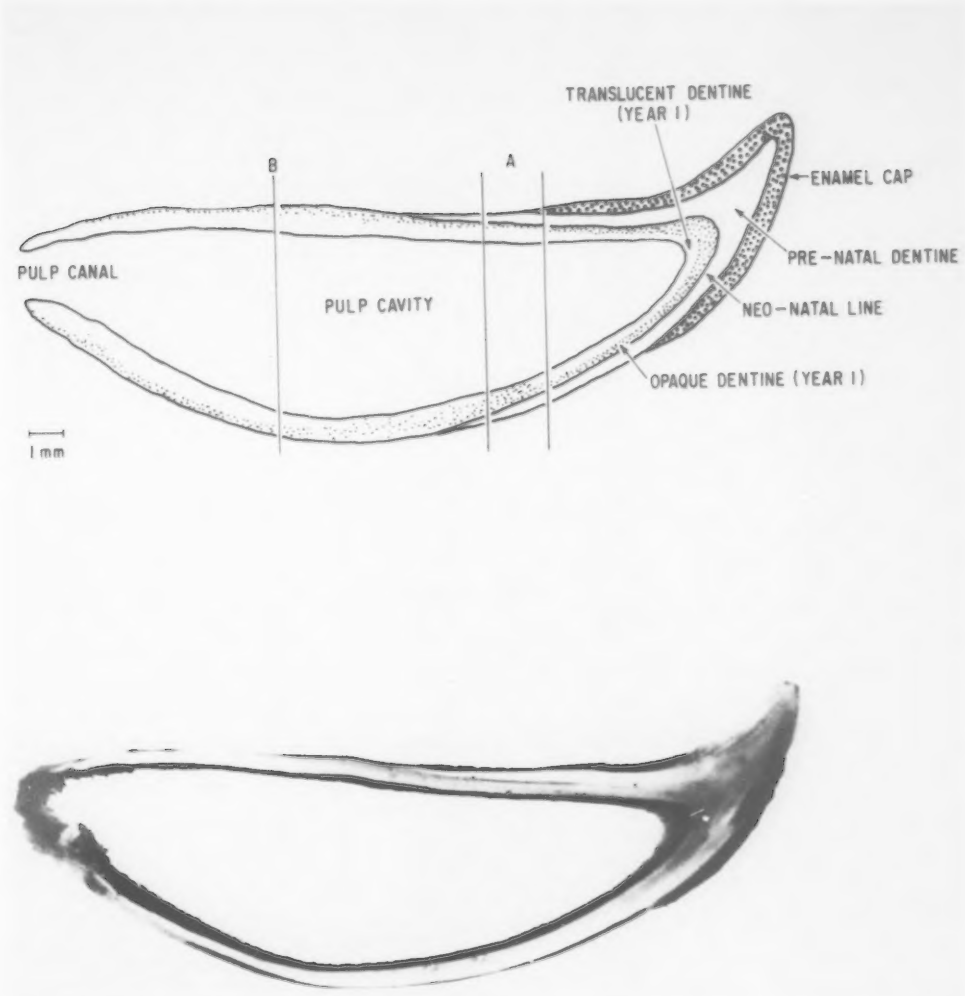

FIG. 1. Sagittal section of lower canine of a 13-mo-old female harp seal.

point in making a judgment about the extent of the 1st-year growth. The neonatal line results from a discontinuity in the growth of dentine which occurs at birth in many mammals. It is usually distinct in transverse sections. The position of the neonatal line in a transverse section will depend on the location from which the section was taken, and will not appear in a section taken close to the proximal end of the tooth, say from position B in Fig. 1. In a transverse section cut from zone A in the distal half of the tooth root (Fig. 1), the neonatal line is located an average of 172 ± 8 μm inside the dentine–cementum junction (Fig. 3A, B).

The thickness of dentinal annuli in transverse sections is shown as a function of age in Fig. 4. The widest dentinal GLG is deposited in the 1st year. Between the ages of 1 and 7+ (7–10) yr there is a linear decrease in the width of successive dentinal GLGs from an average of 489 μm at age 1 to 124 μm at ages 7–10. Although some of the variation in the width of dentinal GLGs can be attributed to variation in the location from which the section was taken, individual variation in dentine growth rate is clearly evident. The thickness of successive dentinal GLGs in nine harp seals is plotted against age in Fig. 5. In only four of these nine animals is the

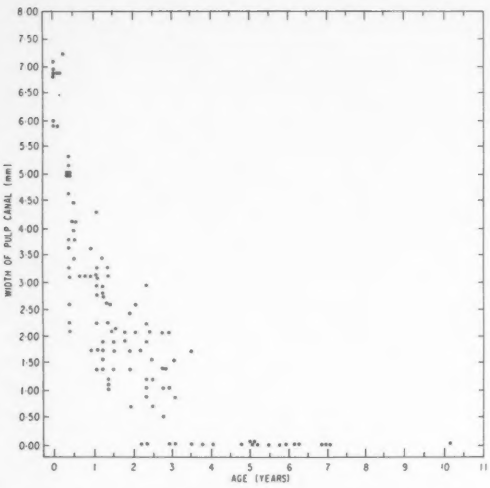

FIG. 2. Decrease in width of pulp canal in lower canine teeth with increasing age in 111 known-age harp seals.

thickness of the first GLG greater than the second and succeeding GLGs. One individual (M964) shows an increase in the width of succeeding GLGs to the age of 4 and another (58) to age 3, with a decrease thereafter. Such variation increases the difficulty of determining true age by making it more difficult to eliminate a false GLG based on its position relative to that of others which are perhaps more distinct.

The total width of the dentine layer from the neonatal line to the edge of the pulp cavity increases linearly with age from 6 mo to 10 yr (Fig. 6). However, this linear growth cannot be expected to continue, as there is only a finite amount of space inside the tooth. Examination of teeth from harp seals of unknown age suggests that the total thickness of the dentine continues to increase beyond the age of 25 yr, at which point the width of incremental growth in the dentine is quite small and magnification of 50× or more may be required to resolve individual GLGs. The pulp cavity in harp seal canines is usually not completely filled with dentine until 25 to 30 GLGs have been deposited, and as many as 34 to 37 GLGs have been resolved in several specimens (Fisher 1954; W. D. Bowen unpublished data).

Evidence for Annual Nature of GLGs

To establish when the various IGLs are formed, it is necessary to observe the nature of the newly formed dentine next to the pulp cavity, in seals killed at all times of the year. There is good seasonal representation of known-age animals among age groups 0 to 2 in the present sample. The thickness of the translucent IGL next to the pulp cavity was measured in 91 specimens. Because the absolute growth increment of dentine is a function of age, within each age group, measurements were standardized by dividing each value by the maximum value in that age group. The resulting scores, ranging from 0.0 to 1.0, were then plotted by month for each age (Fig. 7).

The relative thickness of translucent dentine by July–August in the 1st year is greater than that in the 2nd and 3rd years. However, at each age the translucent IGL begins to form in June–July and reaches its maximum thickness in February–March, corresponding to the time of harp seal births. The outermost IGL in a typical GLG, the interglobular dentine, is formed in April and early May, the period when harp seals undergo their annual molt. The middle IGL or opaque band is formed in May and June, during the time when most harp seals are migrating to their summer feeding range (Fig. 7). There is also an indication from the data on 2nd- and 3rd-year growth of the translucent IGL, that the growth rate of this layer is not constant throughout the year. The most rapid growth appears to occur in winter from January to March (Fig. 7), during which time the seals are feeding heavily. However, more data are required to confirm this.

The annual nature of dentinal GLGs in harp seal canines is illustrated further in Fig. 3A to H. The neonatal line is clearly seen in Fig. 3A, B, and E. At the end of the 1st year of growth, the dentine consists of an outer opaque IGL and a wide inner IGL of translucent dentine (Fig. 3B). Interglobular dentine is deposited during the annual molt in April (Fig. 3C). By late August the second GLG consists of the layer of interglobular dentine and an opaque layer (Fig. 3D), and by December the second GLG consists of all three IGLs (Fig. 3E). A false GLG can also be seen in Fig. 3E. Figure 3F, G, and H illustrate the pattern of GLGs in the dentine in animals ranging from 2 yr and 9 mo to 10 yr and 1 mo of age.

Accuracy of the Method

We next consider how accurate and consistent are ages determined from transverse sections when the actual age of the animal is unknown to the observer.

To examine the accuracy and precision of age determined by counting dentinal GLGs, one of the authors (W.D.B.) estimated the ages of 138 known-age harp seals in five blind replicates. Replicate examinations were done prior to detailed study of the dentinal GLGs of the known-age sample to minimize familiarity with the material.

The results of this experiment are summarized in Table 2. Overall, 83.4% of 675 'readings' resulted in assigning the correct age. However, because the teeth examined were mainly from young animals, the accuracy of the method over a wider range of ages is undoubtedly overestimated. The probability of estimating the age of harp seals correctly varied between ages and generally decreased with age. Only 0.724 of estimates of 0-group seals were correct using only transverse sections as the basis for the determination. Errors generally consisted of counting false annuli near the pulp cavity in animals 9–11 mo of age. However, these errors were virtually eliminated (0.99 correct determinations) when the tooth root was also examined. In animals less than 1 yr of age the pulp canal is generally $\geq$3.0 mm in diameter and the root has a translucent appearance, resulting from the rather thin layer of dentine that has been deposited. By contrast, in animals 1 yr and older, the pulp canal is usually $<$3.0 mm in width and the root is opaque. At ages 1 and 2 yr, 0.983 and 0.889, respectively, of readings based on transverse sections resulted

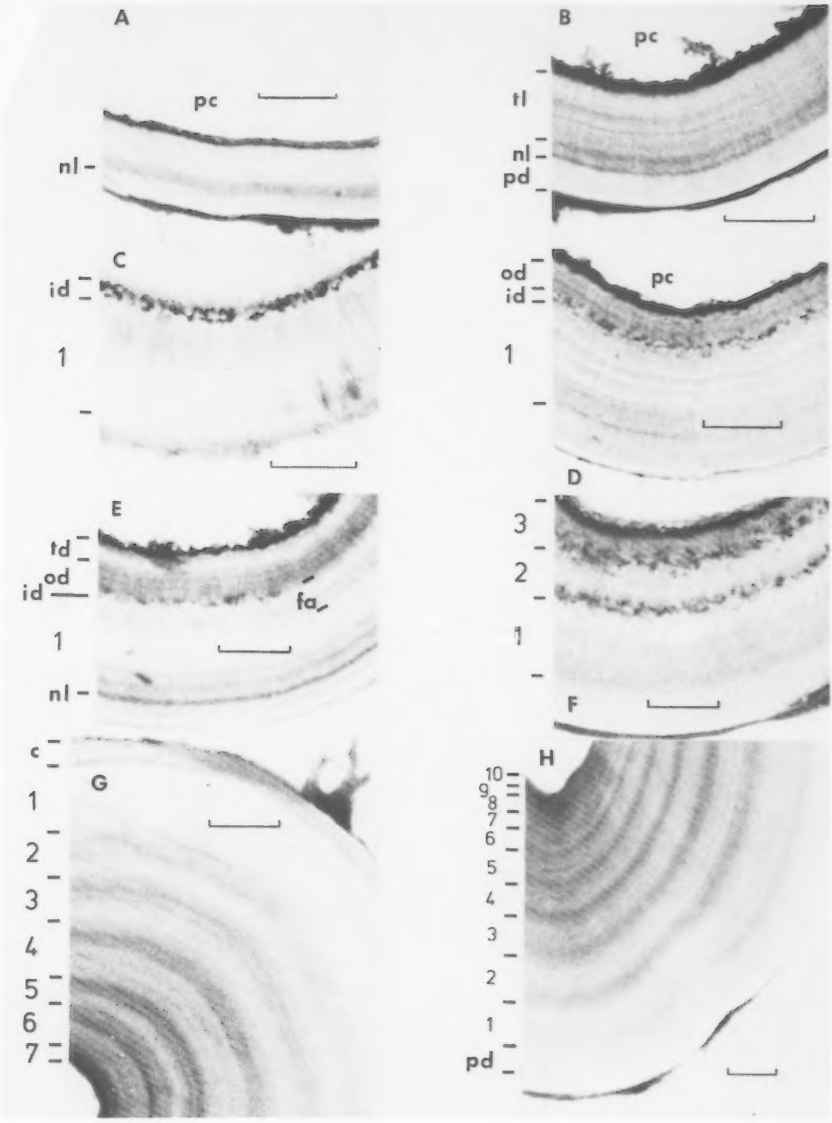

FIG. 3. Transverse canine sections of known-age harp seals examined with transmitted light. Bar scales = 0.5 mm (i.e. magnifications are from about 20 to 30×). (A) A 5-mo-old animal, killed August 11, 1980, (B) An 11-mo-old seal, killed February 10, 1979, (C) A 13-mo-old seal, killed April 18, 1969, (D) A 1½-yr-old seal, killed September 1, 1979, (E) Harp seal 1 yr and 9 mo of age, killed December, 1979, (F) Harp seal 2 yr and 9 mo of age, killed December, 1980, (G) Female harp seal age 6 yr and 11 mo, killed February 18, 1982, (H) Male harp seal age 10 yr and 1 mo, killed April 25, 1982. c, cementum; fa, false GLG; id, interglobular dentine; nl, neonatal line; od, opaque dentine; pc, pulp cavity; pd, prenatal dentine; td, translucent dentine. Numerals denote annual GLGs.

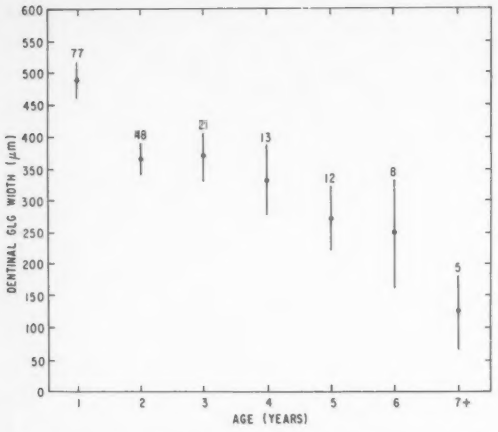

FIG. 4. Decrease in the average thickness of dentinal GLGs in the lower canines of known-age harp seals with increasing age. Vertical lines are 95% confidence intervals and numerals are sample size.

in the correct age being assigned. Age was estimated correctly in only 0.700 of 3-yr-olds. However, the age of two specimens, whose known age was 3 yr, was estimated consistently at 2 yr. Careful examination of both teeth revealed two complete GLGs and a third incomplete GLG, thus making these animals 2-yr-olds. It is likely that an error in tag-tooth association had been made in these cases. In three other cases the wrong tooth was clearly associated with the tag; a 1-yr-old read age 4, and two 8-yr-olds read age 4 and 18–22, respectively. Eliminating the above two specimens, as errors in tag-tooth association, then 49 of 60 or 0.817 (rather than 49 of 70 as in Table 2) of readings of 3-yr-olds resulted in correct age determination. Beyond age 3 yr, the existing data are insufficient to estimate the accuracy of age determined by counting GLGs. Although pooling ages 4 through 10 suggests that only about 0.553 of determinations would be correct, the age of all three 4-yr-old animals was estimated correctly and four of five readings of the 10-yr-old animal (Fig. 3H) were correct (Table 2).

Various rules could be used to decide upon the age of an individual animal using dentinal GLGs. In routine age determination for population dynamics it is usual to base the age of individuals on the result of a single examination of a transverse section. The above estimates of accuracy are what can be expected on average based on this method. However, we could adopt a rule which took, for example, the average of five readings (rounded to the nearest year) as the correct age. Following this method (and this is only one of many that could be proposed), the probability of correctly determining the age of a single animal is 1.00, 0.889, 0.833, and 0.625 for ages 1, 2, 3, and 4+, respectively. These values are slightly higher than those based on a single reading.

We have omitted further consideration of 0-group seals for two reasons. First, their age is based more on examination of the tooth root than on examination of dentine and second, they are usually killed in the commercial hunt at a time when their age can be determined with considerable certainty by body size alone. Thus as a rule, it is not necessary to estimate their age.

Variation in estimated age about the true age can be expressed by the relative percentage error (RPE), defined as:

$$(1)\quad \mathrm{RPE} = \frac{\left(\dfrac{\sum_{i}^{n}(x_i - \mu)^2}{n}\right)^{1/2}}{\mu} \times 100$$

where x_i is the ith reading of n readings and μ is the true age. For example, at age 1 yr there are 235 readings (Table 2). The RPE is 13.0, 16.7, and 14.3% at ages 1, 2, and 3 yr, respectively. Although sample sizes are small beyond age 3 yr, there is no indication of a trend in the RPE with increasing age (Table 3). However, more data are required to confirm this result. In addition to inconsistency in age estimation, there is also a potential bias in determining age by counting dentinal GLGs. The age of young animals tends to be overestimated and that of older animals (ages 5, 6, and 7) underestimated (Table 2).

Discussion

Our results demonstrate the annual nature of dentinal GLGs in the canine teeth of harp seals. In the 1st year two IGLs are deposited and, in most specimens, three IGLs are formed annually thereafter. Fisher (1954) described each GLG in the canine teeth of harp seals as consisting of two parts, an outer layer of reticulate air spaces (interglobular dentine) and an inner layer of opaque dentine. According to Fisher, these IGLs were separated by "areas of clear 'normal' looking dentine." Although Fisher's terminology differs somewhat from that which we have used, the pattern described is similar. This pattern also corresponds to that observed in ringed seals, *Phoca hispida* (McLaren 1958; Smith 1973); crabeater seals, *Lobodon carcinophagus* (Laws 1958); and hooded seals (T. Øritsland unpublished data). The interglobular dentine layer is absent in about 38% of known-age harp seal teeth examined. In these cases, each dentinal GLG consists of an outer opaque IGL and an inner translucent IGL. Variation in the presence of interglobular dentine (also known as vacuolated or reticulate dentine: Fisher 1954; McLaren 1958; Laws 1958, 1962) has also been noted in ringed seals (McLaren 1958) and hooded seals (W. D. Bowen unpublished data). Similar patterns of dentinal laminae are found in the leopard seal, *Hydrurga leptonyx*; the Weddell seal, *Leptonychotes weddelli*; and the Ross seal, *Ommatophoca rossi* (Laws 1962).

The results of this study show that the opaque IGL is formed during the period May to perhaps early July (Fig. 7). This corresponds to the northward migration of harp seals. Lacking known-age material, Fisher (1954) concluded that "the dark or opaque layer is laid down at some time between the moult and the beginning of the southward migration, probably during the summer sojourn in the Arctic." Rasmussen (1957) stated that white (translucent) zones in the dentine are formed in feeding periods, mainly during the summer, and that the dark layers are formed in periods when

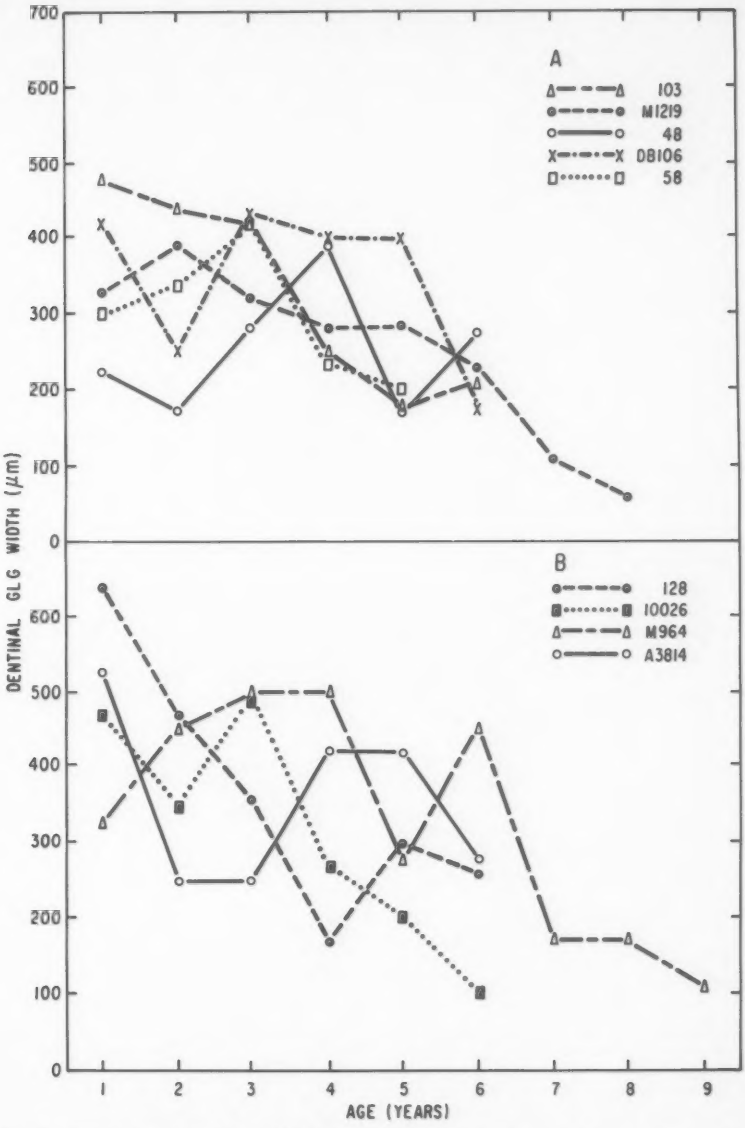

FIG. 5. Individual variation in the width of dentinal GLGs in lower canines as a function of age in nine known-age harp seals.

the animals do not feed, such as during whelping and molting. We conclude that the opaque IGL is deposited more quickly than assumed by Fisher and somewhat later than assumed by Rasmussen.

Yakovenko (1960) stated that a layer of clear dentine is formed during such times as whelping or molting when harp seals are hauled out upon the ice. A dark layer of dentine is formed during the summer and winter periods when animals are in the sea. The contradictory nature of these observations is resolved by noting that the optical density of dentinal IGLs under reflected light is opposite to that seen under transmitted light. Yakovenko examined his material under reflected and

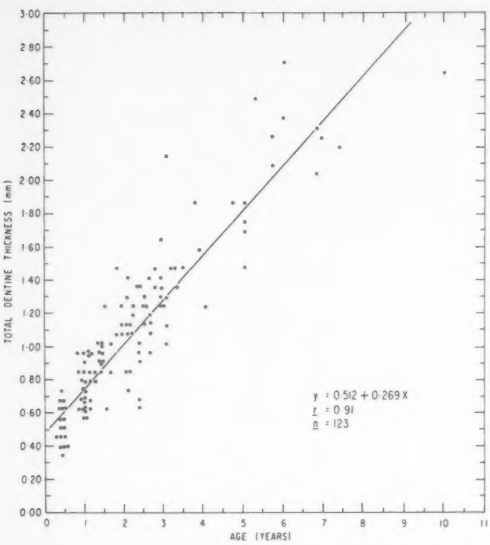

FIG. 6. Relationships between total dentine thickness and age in 123 known-age harp seals.

not transmitted light as was used by Fisher, Rasmussen, and in this study.

Our measurements of the thickness of dentine deposited during the 1st and 2nd year of life are lower than those reported by Fisher (1954). Based on 27 animals of unknown age, Fisher found that 0.7 mm (700 μm) of dentine was deposited from 1 mo of age to the beginning of the first layer of interglobular dentine. This compares with only 489 μm of dentine from birth to the end of 1 yr in our study (Fig. 4). During the 2nd year, Fisher reported that 0.8 mm (800 μm) of dentine was deposited compared to 370 μm in this study. Our measurements of 3rd-year growth (≈ 400 μm) and those of Fishers agree. Furthermore, our data show that the growth of dentine in the 1st year is significantly greater than in the 2nd year of life. This is also the case in ringed seals (Smith 1973). However, Fisher found no difference between the thickness of dentine formed in the 1st and 2nd year of life.

The reasons for this discrepancy are not clear. One possibility is that on average, Fisher sectioned his samples further toward the distal end of the tooth root where the dentine would be thicker. However, if this were the case then we should expect a systematic difference in all GLGs, which was not found. Another possibility is that the growth rate of harp seals born in the early 1950s was greater than that of seals born in the late 1970s. However, this hypothesis is not supported by the limited available data on long-term trends in harp seal growth rate; if anything the reverse seems more likely (Innes et al. 1981). We conclude that the thickness of the first and second GLGs was greater in the 1950s than in the 1970s. However, it is not possible to account for these differences at present.

The factors responsible for the formation of IGLs in the

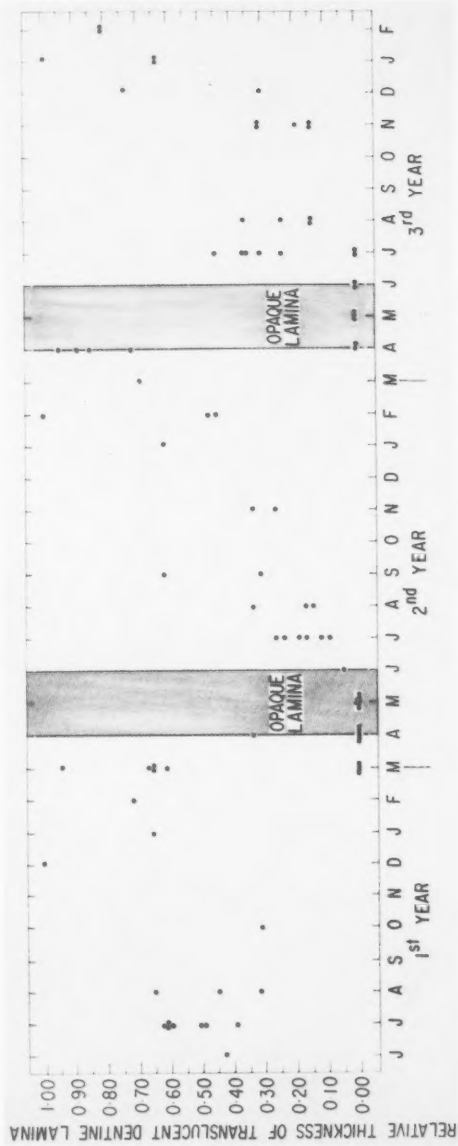

FIG. 7. Monthly variation in the relative thickness of translucent dentine next to the pulp cavity in 91 known-age harp seals between the ages of 4 mo and 36 mo. See text for detail.

TABLE 2. Comparison of estimated and actual age of 135[a] harp seals. Each tooth read five times in blind replicates. Proportion of correct determinations given in parentheses.

Actual age (yr)	Estimated age (yr)												
	0	1	2	3	4	5	6	7	8	9	10	Readings	*n*
0	76 (0.724)[b]	29										105	21
1		231 (0.983)	4									235	47
2		9	160 (0.889)	11								180	36
3			20	49 (0.700)[c]	1							70	14
4					15 (1.00)							15	3
5					18	15 (0.429)	2					35	7
6					1	6	12 (0.600)	1				20	4
7						1	8	1 (0.143)				10	2
8													
9													
10										1	4	5	1
Total												675	135

[a]Three of 138 teeth examined were eliminated because of wrong tooth or wrong known-age information.
[b]0.990% if tooth root also used, see text.
[c]0.817% if two problematical teeth eliminated, see text.

TABLE 3. Age-specific estimates of relative percentage error of age determined by counting dentinal GLGs in harp seal canine teeth.

Known age (yr)	*n*	Relative percentage error
1	47	13.0
2	36	16.7
3	12	14.3
4	3	0.0
5	7	15.1
6	3	7.4
7	2	15.6
10	1	4.5

dentine of harp seals and in other mammals are poorly understood; however, a number of hypotheses have been proposed. These include seasonal variation in hormone balance (Carrick and Ingham 1962), in vitamin D levels (Mellanby 1928; Laws 1953; Fisher 1954; McLaren 1958), and in nutritional state or feeding intensity (Mansfield 1958; Scheffer 1950). Scheffer and Peterson (1967) found a direct correlation between nutrition and postnatal dentinal layering in suckling pups of the Alaskan fur seal. Kubota et al. (1961) felt that differential calcification of the dentine in the canine tooth of fur seals reflects alternating periods of normal and disturbed calcium metabolism, which in turn reflects the nutritional state of the animal. For example, a deficiency of vitamin C leads to a reduction in dentinal deposition rate and subsequent hypercalcification (Symons 1967), and deficiency of vitamin A causes the formation of interglobular dentine in rats (Rowles 1967).

Another explanation is that endogenous factors are largely responsible for discontinuous growth. Grue and Jensen (1979) reviewed the available data on 52 species of terrestrial mammals and concluded that the formation of IGLs is governed to a considerable degree by internal rhythms which are coupled to the animal's overall pattern of growth and metabolism. Gaskin and Blair (1977), in their study of the harbor porpoise, *Phocoena phocoena*, concluded that the timing of zone deposition is in some way determined by the date of birth, and maintained by an annual endogenous cycle.

IGLs in the dentine of harp seals and certain other phocids are associated with rather specific events in the annual cycle (Fisher 1954; Rasmussen 1957; Laws 1958, 1962; this study). The deposition of well-calcified dentine in the teeth of odontocetes and many other mammals is generally attributed to good nutrition, whereas poorly mineralized dentine is deposited when feeding is reduced to suboptimal levels or as a result of metabolic disturbances for other reasons (Sergeant 1959, 1962; Johansen 1967). In harp seals interglobular dentine, which is poorly calcified but optically dense in transmitted light (Symons 1967), is deposited in the molting season (Fisher 1954; this study), a period of 3 or 4 wk when little if any feeding occurs. Laws (1958) estimated that interglobular dentine in the canine tooth of crabeater seals is deposited in the period September to October, probably during the pupping season in September. This is also at a time of reduced feeding.

The opaque IGL in harp seal canines is deposited from May to early July during the spring migration. Although the feeding habits of harp seals at this time of the year are not well known, some feeding does take place (Foy et al. 1981). The translucent IGL is formed largely from January to March when harp seals are feeding heavily. Therefore, we might expect that the dentinal GLG would represent a series of layers of increasing mineralization. However, there is considerable conflicting evidence on the relationship between optical opacity, mineral content, and other physicochemical properties of dentine (Hay 1980). For the present, it is not possible to say which of the two inner IGLs is more highly calcified.

The decision as to which features are included in the count as GLGs is made on the basis of an inspection of the overall pattern of dentinal layering, rather than strictly on the basis of the internal structure of the dentine. Inevitably a certain subjective skill is involved in determining age by counting GLGs (Gambell 1977). Therefore, it may be expected that an incorrect age will be determined in a certain proportion of samples examined.

In general, few attempts have been made to assess the accuracy of age estimation procedures (Dapson 1980). The present known-age material is insufficient to estimate the accuracy and precision of the method much beyond the age of 3 yr. Taking the mean of five readings, the probability of correctly estimating the age of an animal decreases with age from 1.0 at age 1 yr to 0.83 at age 3 yr and based on a small sample, to 0.63 at age 4+ yr. Similar results were obtained by Doubleday and Bowen (1980) who studied a sample of 202 canine teeth from harp seals of unknown age. As in the present study, each tooth was examined in five blind replicates by W.D.B. Age was assigned on the following basis: if three or more readings were the same, this value was assumed to be the 'actual' age, and if less than three readings were the same, the mean value was taken as the 'actual' age. They found that the probability of a single age reading being equal to the mean age decreased linearly from 1.0 at age 1 to about 0.2 at age 22. Our results demonstrate, however, that this previous work overestimated the accuracy of age determination based on GLGs. It is clear that repeated examinations of certain teeth are consistent but wrong. Of 22 teeth in which one or more of five readings differed from the true age, 27.3% consistently differed. When the true age of the animal is unknown this type of error cannot be detected.

The bias in age estimation reported herein has been found in other studies. Anas (1970), studying a large sample of known-age northern fur seal canines, found a clear tendency for readers to overestimate the age of 3- to 5-yr-old females and to underestimate, by as much as 70% of the time for one reader, the age of 6- to 10-yr-olds. Doubleday and Bowen (1980) demonstrated that age reading variations can bias estimates of harp seal pup production (using the survival index method) by as much as 10% and natural mortality rates from catch curves by a comparable amount. Inconsistencies in age determination also tend to overestimate mean age of maturity. They concluded that the size of these biases is sufficient to have an impact on management advice for northwest Atlantic harp seals. However, Doubleday and Bowen did not consider error caused by consistent but inaccurate age determinations. Hence the impact of age determination errors on the management of harp seals will likely be greater than that previously anticipated.

Acknowledgments

We are grateful to W. Penney, W. Hoek, and B. Bergflødt for cutting thin sections of the known-age teeth. F. Kapel provided much of the material collected during the summer period. H. Mullett drafted the figures. We thank K. Hay, D. H. Fisher, and two referees for commenting on earlier drafts of the manuscript.

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Survival Value of An Opportunistic Life-stage Transition in Capelin (*Mallotus villosus*)

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FRANK, K. T., AND W. C. LEGGETT. 1983. Survival value of an opportunistic life-stage transition in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 40: 1442 – 1448.

We examined the biological basis of the synchrony between the onset of a pelagic existence in beach-spawned capelin (*Mallotus villosus*) larvae and the unpredictable occurrence of favorable predator–prey conditions caused by onshore winds. Larvae isolated from the in situ beach sediments, but subject to those changes in water mass characteristics as might remain when such water is introduced into an experimental constant-level tank, emerged in synchrony with larvae in situ. This supports the hypothesis that the larval response to wind-induced water-mass exchange is an active one; it represents an adaptation maximizing feeding success and minimizing mortality due to predation. This "opportunistic" life-stage transition has direct parallels in seed dormancy and diapause in insects.

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Le présent article contient un examen du fondement biologique du synchronisme entre le déclenchement d'une existence pélagique de larves de capelan (*Mallotus villosus*) provenant d'oeufs déposés sur la plage et l'occurrence imprévisible de conditions favorables de prédateur–proie causées par des vents du large. Des larves isolées de sédiments de rivage *in situ*, mais soumises aux changements de caractéristiques de masse d'eau encore présentes quand cette eau est introduite dans un bassin expérimental à niveau constant, émergent en même temps que les larves *in situ*. Ceci appuie l'hypothèse que la réaction des larves à un échange de masse d'eau provoqué par le vent est une réaction active; elle est une adaptation portant au maximum le succès de l'alimentation et minimisant la mortalité par prédation. Cette transition « opportuniste » dans le cycle de vie est comparable à la dormance des graines et à la diapause des insectes.

Received February 1, 1983
Accepted June 1, 1983

Reçu le 1 février 1983
Accepté le 1 juin 1983

SUCCESSFUL early development of many plant and animal species necessitates the timing of various life phases to periodically occurring environmental conditions. Seed dormancy, insect diapause, and the rapid and synchronous emergence from these states are examples of how organisms avoid unfavorable conditions and then respond appropriately to environmental cues correlated with the arrival of an environmental condition that yields a high survival probability. The timing of such occurrences may be predictable or unpredictable and the required responses may induce considerable differences in life history strategies (Levins 1968).

Marine fishes often show one or more periods during which individuals act synchronously. Examples include spawning, hatching, larval dispersion, first feeding, and small- (diel-vertical) and large-scale (migratory-horizontal) movements. Environmental events are most often thought to act as cues. Synchronous responses to the environment are generally interpreted as strategies that increase fitness and are maintained by natural selection. Some species synchronize life-stage transitions to the occurrence of cyclical, highly predictable environmental events. Examples include the diurnal patterns of larval emergence from the spawning beds by salmonids and the vertical migration of larval clupeids, both of which are believed to enhance predator avoidance and food acquisition (Bams 1969; Wood 1971; Seliverstov 1974). The synchrony between hatching time and larval dispersal in atherinids and lunar cycles (Walker 1952) presumably confers similar survival advantages.

Being in the right place, at the right developmental stage, and at the right time is a more complex problem for species in which stochastic events regulate environmental quality and survival. The precarious synchrony between timing of transi-

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Printed in Canada (J7235)
Imprimé au Canada (J7235)

tion from endogenous to exogenous feeding in pelagic fish larvae and peaks in plankton abundance (Hjort 1914, 1926; Cushing 1974, 1975; Jones and Hall 1974; Ware 1977) is one of the most cited examples of the importance of achieving synchrony to individual fitness and population stability, in spite of the temporally unpredictable nature of the environment. Adaptive relationships between early life history traits and stochastic features of the environment have not been as extensively studied. Recently, meteorological and hydrographic phenomena have become recognized as important stochastic regulators of biological processes in the seas. Examples of such regulators include the extremes of wind intensity that influence the formation of chlorophyll maxima layers, and the concentrating effect of Langmuir cells on microzooplankton. Both effects promote detection by, and successful initiation of, first feeding in northern anchovy *Engraulis mordax* (Lasker 1981), and Peruvian anchoveta *Engraulis ringens* (Ware et al. 1981). The importance of wind-mediated Ekman transport of larval Atlantic menhaden (*Brevoortia tyrannus*) to their coastal nursery areas (Nelson et al. 1977) presents another example. We have recently shown (Frank and Leggett 1982b) that emergence of larval capelin (*Mallotus villosus*) from their beach gravel incubation sites, and initiation of larval drift, are strongly linked to the irregular occurrence of infrequent onshore winds. The linking of the onset of larval drift to the occurrence of onshore winds is believed to favor survival by causing the initial stages of drift, and first feeding, to occur when predator–prey relationships are most favorable (Frank and Leggett 1982b).

Critical life-stage transitions can have profound effects on abundance. Synchrony, or the lack thereof, is believed to be one of the major regulators of variations in year class strength, characteristic of many pelagic spawning marine fishes (Hjort 1914; Lasker 1981; Cushing 1974, 1975; Sette 1943; Dragesund 1969). Determining the key regulators of survival during critical life stages is central to long-range forecasting.

This paper reports investigations into the biological basis for the synchrony between onset of larval drift in capelin and occurrence of favorable feeding and predator conditions.

Materials and Methods

Capelin

During mid-June to early July capelin spawn along Newfoundland and Labrador's east coast on exposed beaches at the heads of embayments. The adhesive eggs are distributed over the breadth of the intertidal zone, to depths exceeding 15 cm, at densities ranging from 90 to 150 eggs/cm^3. During the 2- to 3-wk incubation period eggs and larvae can be easily studied by sampling the beach gravel. Average size at hatching is 4.9 mm. Emergence of larvae from the beach is a clearly defined, abrupt transition to a pelagic existence.

We have previously shown (Frank and Leggett 1981b, 1982a) how hydrographic and meteorological conditions influence embryonic development rate, preemergent larval growth rate and growth efficiency, and the physical condition of larvae at the onset of drift. Larval emergence is strongly linked with the irregular occurrence of infrequent onshore winds, which generate wave action possibly capable of flushing larvae from the gravel. Larvae accumulate in the sediments during the intervals between the infrequent onshore winds (Frank and Leggett 1981a). Onshore winds replace cold, food-poor, predator-laden, upwelling waters, which occupy the nearshore areas during offshore winds, with warmer, food-rich, predator-deficient surface waters (Frank and Leggett 1982b). The resulting association with enhanced food resources can result in a doubling of growth rates over what would be achieved if emergence were continuous. Several authors have argued that rapid early growth significantly reduces the time larvae are susceptible to planktonic predators. Synchronous release of larvae at very high densities may also enhance survival due to predator swamping (Frank and Leggett 1982b).

Hypotheses

There are two possible mechanisms that could lead to the synchronizing of larval emergence and the initiation of drift with the occurrence of onshore winds. Our first hypothesis is that larval emergence is passive. Deep burial of eggs would impose a physical restraint on emergence during periods of offshore winds when the nearshore area is characteristically calm. Onshore winds create wave action and physical disturbance of the beach area, which would promote passive flushing of larvae from the sediments into the nearshore pelagic area. Alternatively, larval emergence could be active. Under this hypothesis capelin larvae would be capable of escaping the beach sediments during periods of offshore winds, but inhibited until stimulated to do so by environmental cues associated with the occurrence of onshore winds. One conspicuous and consistent cue might be the sharp increase in temperature associated with such a water mass replacement.

Approach

The study was conducted at Bryant's Cove, Nfld. (47°40′36″N; 53°11′24″W). A physical description of the area is contained in Frank and Leggett (1981a).

We sought to evaluate the active dispersal hypothesis by supplying all environmental factors present during normal incubation, hatching, and dispersal of larval capelin with the exception of the wave and tide induced changes in the rearing environment. Five identical clear Plexiglas aquaria (14 cm wide × 30.5 cm long × 30.5 cm high) were installed in one room of our on-site laboratory. Each tank was fitted with a 1-cm-diameter adjustable flow surface inlet and a drain, located at opposite ends of the tank. The inflow pipe could be adjusted to maintain water levels while the tanks were continuously flushed with seawater drawn from the area adjacent to the spawning beach. Inlet and drain pipes were fitted with 150-μm stainless steel mesh screens.

The beach spawning environment was simulated in each of the tanks. Egg-laden beach gravel was collected on June 19, 1981, 2 d after an intense bout of beach spawning and placed in a 6-cm deep layer in each of the aquaria. This egg/gravel mixture rested on a 4-cm base layer of clean (washed in seawater and sun-dried) egg-free beach gravel. A 2-cm deep layer of washed and dried egg-free gravel was placed over the

egg layer to avoid passive emergence of larvae at the sediment/water interface.

A single-stage jet pump located near the water edge drew water from a location 15 m offshore and 2–3 m below the surface depending on the tide. The intake was a sealed 30-cm square box with two 8-cm-diameter portholes that were covered with 150-μm stainless steel mesh screening. The hose leading from the pump to the laboratory (20-m distance) was partially buried and was wrapped in aluminum foil to reduce solar heating. Water temperatures in the tanks tracked those in the nearshore environment, but throughout the experiment, tank temperature was 0.8°C (SE = 0.24) higher than that in the cove.

Prior to hatching, flow to the tanks was interrupted and the tanks drained twice daily to simulate the repeated exposure and inundation of the beach spawning sites due to tidal action. Once hatching had begun and larvae began to leave the gravel, constant flows were maintained at rates sufficient to maintain a 15-cm deep layer of water over the sediment. No disturbance of the egg and gravel mixture resulted from water movement in the tanks. Air temperatures in the laboratory were allowed to track outside air temperatures throughout the experiment. Lights were automatically turned on at 06:00 and off at 20:00 to coincide with the ambient light cycle. We have, however, previously shown that larval emergence is independent of the light regime (Frank and Leggett 1981a).

Sampling of eggs and larvae from the sediments was accomplished by coring with a smaller version (2 cm ID × 14 cm long) of a coring device routinely used to sample the egg/gravel mixture in the field (Frank and Leggett 1981b). Each core sample was sectioned into 2-cm intervals and preserved in 4% formalin. This yielded data on egg and larval densities by depth stratum in each tank, and proportions of live and dead eggs. Cores were taken from each tank at the outset and the termination of the experiment to yield information on changes in egg numbers, egg mortality, and the numbers of larvae remaining in the sediments.

We collected emerged larvae by sweeping a fine mesh 15 cm × 13 cm net repeatedly through the water column parallel to the gravel bed along the long axis of the tank until all the larvae were captured. Collections were made at least twice daily throughout the experiment and during periods of peak emergence every 3 h. All larvae were preserved in 4% buffered formalin and were subsequently measured. Total length measurements were made to the nearest 0.05 mm and yolk sac size was rated according to a five-point scale (4, full yolk sac; 0, no yolk sac; see Frank and Leggett 1982a). Only the full and no yolk categories are presented in the text. Larval emergence was expressed as a time-dependent rate, e.g. as number of larvae per hour or day.

Throughout the experiment we monitored larval emergence rates in the bay. A 0.5-m-diameter standard plankton net fitted with a 153-μm mesh net and a General Oceanics flowmeter was towed parallel to and 15 m distant from the

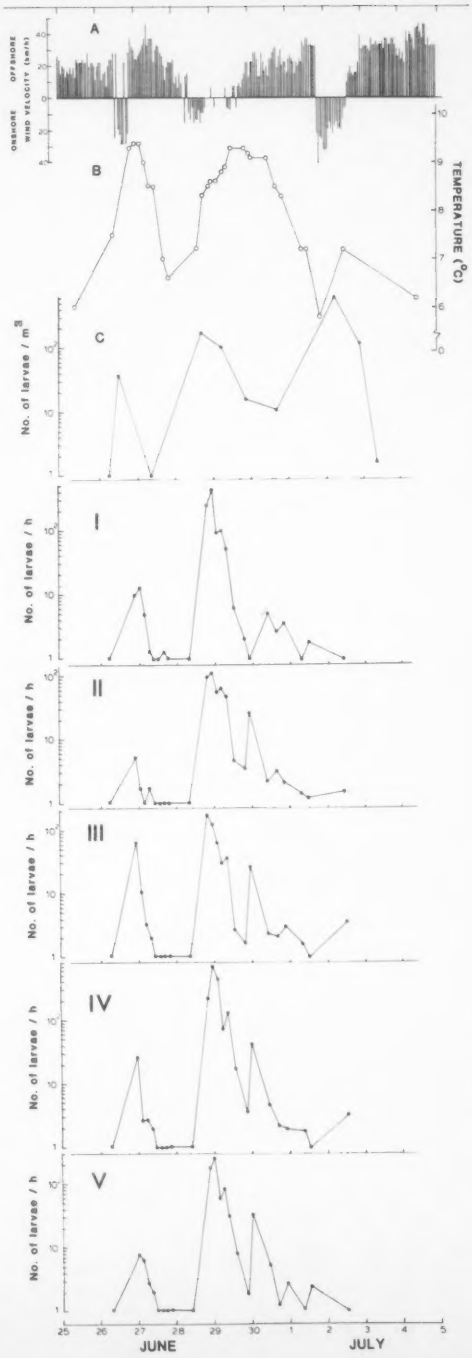
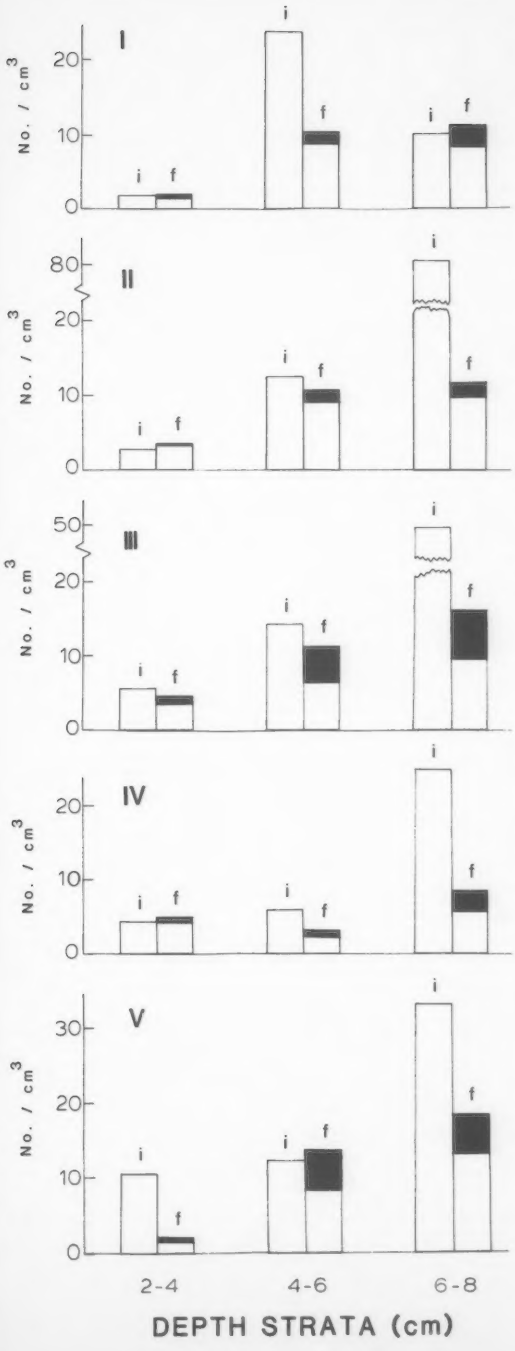


FIG. 1. (A) Hourly wind speed and direction. Offshore and onshore wind directions are indicated by lines above and below the zero line, respectively. (B) Water temperature in the 1- to 2-m depth stratum at the Bryant's Cove study site. (C) Density of emerged capelin larvae collected in the nearshore zone, adjacent to the spawning beach. (I–V) Rate of larval emergence from the five experimental tanks.



spawning beach at a speed of 1.2 m/s. Daily or twice-daily collections were made in this manner. Water temperatures were measured at 1-m depth in the area traversed by the plankton net.

Results

The emergence of larval capelin in the bay was strongly linked to the occurrence of onshore winds (Fig. 1A, C), which caused coastal water mass replacement as indicated by pronounced and rapid temperature increases (Fig. 1B). Emergence of capelin larvae in the experimental tanks was synchronous with the emergence pattern in the bay. The data from all five tanks exhibited dramatic and pronounced peaks in the numbers of emerged larvae associated with water mass exchanges resulting from the first two onshore wind events occurring during the experiment (Fig. 1). The low level of emergence during the third onshore wind event presumably was due to restricted numbers of larvae remaining (Fig. 2). The third peak in emergence occurring in the field may have been caused by different temperatures occurring in the low, mid, and high tide zones on the beach. We calculated temperatures for each of these zones from empirical relationships (Frank and Leggett 1981b) and established that temperatures at the high tide level were greater, on average, by 5°C than those at the low tide level. This would have advanced median hatching times by 5 d which agrees well with the difference between first and third emergence.

Emergence of larvae appeared primarily linked to the occurrence of sharp changes in temperature. Other possibilities could lie in an increase in food density and olfactory cues associated with the replaced water mass. Several other possibilities appear less likely. For example, under field conditions larval emergence was shown not to correlate with either light intensity (Kendall's Tau = 0.17, $n = 35$, $P > 0.05$) or tide levels ($R^2 < 0.04$; Frank and Leggett 1981a). A third-order polynomial regression accurately relates the natural logarithm of emergence rates to water temperature ($R^2 = 0.91$, $P < 0.01$; Table 1). In the absence of physical disturbance of the sediments, emergence rates peaked at ~8–9°C and were significantly depressed at both lower and higher temperatures. This observation is consistent with our earlier finding that swimming activity of unconfined larvae reaches an optimum near 8°C (Frank and Leggett 1982a) and suggests that temperature, through its influence on activity, may contribute to the response of larvae to wind-driven water-mass exchanges.

Data obtained through core sampling in the tanks showed little impediment to emergence of larvae from depths of up to 8 cm (Fig. 2). Capelin eggs are naturally buried to depths of 15 cm. Wave disturbance of sediments during onshore winds may facilitate emergence of larvae from these greater depths.

The possibility that synchrony of emergence resulted from preceding hatching synchrony, as is exhibited by the California grunion (*Leuresthes tenuis*) (David 1939; Moffatt and Thomson 1978), can be rejected because capelin larvae emerged at different stages of development. More than 70% of the emerged larvae sampled during the first

FIG. 2. Depth distribution of eggs and larvae in experimental tanks (I–V) at the beginning (i) and end (f) of the experiment. Open bars show egg density, closed bars larval density.

TABLE 1. Polynomial regressions relating water temperature to daily rate of larval emergence from the experimental tanks. Emergence rate was expressed as ln (1 + no. of larvae/d). Analysis of the mean response was based on the arithmetic mean of the five tanks.

Tank	Degree of polynomial	Estimated coefficient for: 1°	2°	3°	$y_{int.}$	R^2	F	P
I	1°	1.788	—	—	−10.678	0.46	5.18	0.063
	2°	10.311	−0.540	—	−43.741	0.48	2.31	ns
	3°	No reduction of SS from previous degree						
II	1°	1.74	—	—	−10.375	0.55	7.30	0.036
	2°	18.043	−1.033	—	−73.617	0.63	4.18	0.086
	3°	−497.721	65.270	−2.819	1253.381	0.86	8.33	0.034
III	1°	2.380	—	—	−15.079	0.73	16.61	0.007
	2°	27.649	−1.601	—	−113.103	0.87	16.29	0.007
	3°	−223.771	30.720	−1.374	533.774	0.91	13.02	0.016
IV	1°	2.501	—	—	−15.915	0.68	12.65	0.012
	2°	29.843	−1.732	—	−121.977	0.81	10.52	0.016
	3°	−340.035	45.816	−2.021	829.675	0.88	9.82	0.026
V	1°	1.944	—	—	−11.966	0.51	6.21	0.047
	2°	No reduction of SS from previous degree						
	3°	No reduction of SS from previous degree						
Mean	1°	1.951	—	—	−11.528	0.60	9.07	0.024
	2°	15.901	−0.884	—	−65.642	0.65	4.66	0.072
	3°	−562.553	73.478	−3.161	1422.649	0.91	13.37	0.015

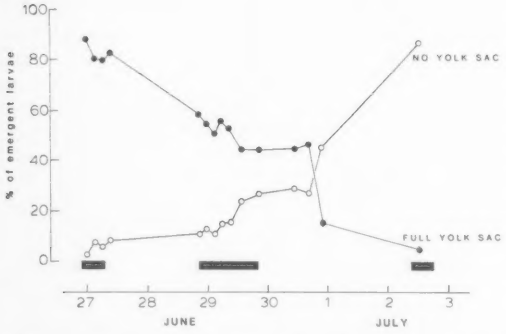


FIG. 3. Temporal changes in the proportion of emerged larvae having full and no yolk sacs. Bars at base of figure indicate the time periods of peak larval emergence from the experimental tanks. Data from all tanks were pooled for this analysis.

emergence peak possessed full yolk sacs, but the proportion of such larvae declined steadily and towards the end ~90% had completely resorbed yolk sacs (Fig. 3). There was a time-dependent increase in larval size ($r = 0.74$, $n = 18$, $P < 0.01$) which averaged 0.4 mm and is believed to have been fueled by the yolk. Yolk sac volumes of emergent beach larvae sampled during 1978–81 revealed a similar pattern, with utilization being a function of the interval since the last onshore wind event.

Discussion

The results of this study support the hypothesis that synchrony between emergence of larval capelin from the beach and occurrence of onshore winds is active rather than passive. Larvae in the experimental tanks emerged in response to changes in water-mass characteristics induced by onshore winds but lacking disturbance by waves and/or tide, in a manner identical with those in the natural beach environment that experienced both water-mass changes and wave and tide action. The experiments do not preclude a possibly additive role of wave action as a facilitator of larval release from the gravel. Increased swimming activity in response to water-mass effects, coupled with displacement due to wave action could, in fact, increase the ease of egress. The very low emergence rates observed in the tanks during offshore winds and in the absence of wave and tide action support this contention (Frank and Leggett 1982b). By selectively leaving the beach gravel during onshore wind conditions the larvae become associated with, and initiate larval drift and first feeding in, a food-rich, predator-poor environment. We have previously shown synchronous, high-density release of larvae to result in predator satiation, which significantly reduced the rate of mortality during the initial stages of drift (Frank and Leggett 1982b).

The shape of the temperature/emergence relationship, and the previously reported (Frank and Leggett 1982a) temperature/swimming relationships for capelin are consistent with the results of previous studies. Bams (1969) observed a precise direct relationship between emergence rate of hatchery grown chum salmon (*Oncorhynchus keta*) larvae from gravel incubators, and temperature over a 5.5–7.0°C range. Both swimming speed and feeding activity were promoted by temperature (range: 13–19°C) in 4-, 6-, 8-, 10-, and 12-d-old northern anchovy larvae (Hunter 1981). Upstream movement of newly emerged salmonid larvae was stimulated

by abrupt increases in water temperature, but depressed by high temperatures [Northcote 1962 (with rainbow trout *Salmo gairdneri*); McCart 1967 (with sockeye salmon *Oncorhynchus nerka*)]. Temperature optima for maximum activity have been observed [Runnström 1957 (for brown trout, *S. trutta*); Houde 1969 (for yellow perch, *Perca flavescens* and walleye, *Stizostedion vitreum vitreum*); Larimore and Duever 1968 (for smallmouth bass, *Micropterus dolomieui*)].

The emergence behavior of larval capelin is also consistent with Cohen's (1967) theoretically derived rules governing the timing of life-stage transitions in unpredictable environments; i.e. (1) organisms should use any prior information about future states of the environment to increase their growth and (2) organisms should select and respond only to those events which transmit relevant vital information (act as an optimum filter by minimizing the noise to signal ratio).

The ecological significance of the larvae's synchronous response to the proximate cues signaling the sporadic occurrence of surface water masses in the nearshore region is twofold: a reduced predator complex may be swamped (Frank and Leggett 1982b), and cooccurrence with abundant food resources is achieved. These circumstances are analogous to the proposed evolutionary forces shaping seed production in some terrestrial ecosystems. For example, selective mortality on seed or seedlings out of phase with the rest of a cohort has been invoked as the causal mechanism initiating the synchronous production of offspring (the result of coevolution with seed predators) in virtually all extratropical hardwoods and conifers (see reviews in Smith 1970; Janzen 1971) and in some tropical tree species (e.g. bamboos, Janzen 1976). Parallels to optimal response to stochastic environmental events are found in the release from dormancy of the seeds of many plant species and the eggs of many animal species during periodic optima in temporally unpredictable environments (Andrewartha 1952; Mayer and Poljakoff-Mayber 1963; Wourms 1972). With capelin, as with other organisms adopting such behavior, the advantages of timing life-stage transitions in synchrony with conditions favorable to survival are not achieved without risk. We have shown the duration of posthatching beach residence is dependent on the rate of yolk absorption which is a finite, variable function of temperature. On average, if the interval between hatching and emergence exceeds 5 d substantial mortality ensues due to exhaustion of yolk reserves. Wind records indicate the average interval between onshore winds in the region during the period of incubation and release to be around 3.5 d (Frank and Leggett 1982b). Fish condition and frequency of release thus seem correlated, at least on average. Variance about the mean is high, which may occasionally lead to catastrophic mortality and significantly depressed year class strength. Greater than 60% of the annual variation in year class strength in capelin over the past 13 yr is explained by the variability in the length of the interval between onshore winds (Frank et al. unpublished data).

Species studied to date in which the timing of critical life-stage transitions is triggered by temporally variable environmental cues appear to achieve considerable independence from the influence of stabilizing biotic regulators of population abundance during their early life history (see review by Giesel 1976). On the other hand, species whose critical life-stage transitions are governed by regularly occurring characteristics of the environment appear to be much more susceptible to predation and other such biotic regulators of population abundance. This suggests that the coefficient of variation in annual recruitment in certain plant and animal populations may, in part, be negatively correlated with the predictability of the timing of the environmental cues governing sensitive early life history transitions. The main mechanism underlying this relationship is the capacity of predators to synchronize their occurrence and abundance with those of their prey.

Acknowledgments

Principal financial support for this research was provided by Fisheries and Oceans Canada, Science Subvention Program. Significant supplementary funding was provided by the Faculty of Graduate Studies and Research, McGill University, and the Natural Sciences and Engineering Research Council of Canada. Logistic and other assistance was provided by the Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St. John's, Newfoundland. We are especially indebted to Dr J. E. Carscadden of Fisheries and Oceans Canada, Messrs Chris Taggart and Francis Juanes, and Mrs Kathleen W. Frank for insights and assistance in various phases of our work. Mrs Susan Bocti contributed to the preparation of the manuscript. We also thank our referees for their contributions to the clarity of the manuscript. Finally, we are pleased to acknowledge, once again, our indebtedness to the residents of Bryant's Cove, Newfoundland. Their hospitality and willingness to assist under any conditions has contributed greatly to the success of our work.

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Use of An Age-Dependent Mark–Recapture Model in Fisheries Research

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POLLOCK, K. H., AND R. H. K. MANN. 1983. Use of an age-dependent mark–recapture model in fisheries research. Can. J. Fish. Aquat. Sci. 40: 1449–1455.

An age-dependent generalization of the Jolly–Seber mark–recapture model for fish populations subject to birth, death, and migration is illustrated using data from a study on northern pike (*Esox lucius*) in Dorset, England. These data show strong evidence of differential survival with age. We estimate the average annual survival rate to be 50% for the pike aged 2 or more years and 34% for those of age 1 yr. We believe that this age-dependent mark–recapture model could be very useful for a wide range of fisheries research and management problems. Often in fisheries work the assumption that survival is independent of age has not been examined critically. We present guidelines helpful in designing mark–recapture studies. This includes a useful design which increases precision and also allows population size estimation to be robust to unequal catchability (heterogeneity or trap response) within an age-class.

POLLOCK, K. H., AND R. H. K. MANN. 1983. Use of an age-dependent mark–recapture model in fisheries research. Can. J. Fish. Aquat. Sci. 40: 1449–1455.

L'article qui suit illustre, à l'aide de données sur le grand brochet (*Esox lucius*) dans le comté de Dorset, en Angleterre, une généralisation dépendante de l'âge du modèle de marquage–recapture de Jolly–Seber pour des populations de poissons soumises à la naissance, à la mort et à la migration. Ces données indiquent clairement des différences de survie en fonction de l'âge. Nous estimons à 50 % le taux de survie annuel moyen de brochets âgés de 2 ans ou plus et à 34 % celui des sujets de 1 an. Nous croyons que ce modèle de marquage–recapture dépendant de l'âge serait très utile pour la solution d'une gamme étendue de problèmes de recherche et de gestion des pêches. Souvent, dans les travaux sur les pêches, on n'a pas examiné de façon critique l'hypothèse que la survie est indépendante de l'âge. Nous présentons des lignes directrices pouvant servir à la conception d'études de marquage–recapture. Ceci comprend un design contribuant à une plus grande précision et permettant également à une estimation d'effectifs de populations d'être valable dans le cas d'une capturabilité variable (hétérogénéité ou réaction à une trappe) au sein d'une classe d'âge.

Received January 11, 1983
Accepted June 2, 1983

Reçu le 11 janvier 1983
Accepté le 2 juin 1983

THE mark–recapture method is widely used in fisheries biology to estimate population numbers, survival rates, and recruitment rates (Cucin and Regier 1966; Ricker 1975; Arnason and Mills 1981). The Jolly–Seber model (Jolly 1965; Seber 1965) is a stochastic (or probabilistic) mark–recapture model for an open population of animals. (By open we mean that the population could be subject to birth, death, and migration processes during the mark–recapture experiment.) This model depends on the assumption that the probabilities of survival and capture are independent of the age of the animal. For an excellent technical description see Seber (1973, p. 196). An intuitive discussion for biologists is given in Pollock (1981a).

Pollock (1981b) developed a model which allows identifiable age-classes to have different survival and capture probabilities. Here the age-dependent model is reviewed and then extensively illustrated using a data set on northern pike (*Esox lucius*) collected from a section of the Frome River in Dorset, England (Mann 1980). We also present some guidelines on designing mark–recapture studies and a discussion of the use of the age-dependent model in fisheries research and management problems.

The Age-Dependent Model

DESCRIPTION

We assume that there is one capture period per "year" for

Printed in Canada (J7196)
Imprimé au Canada (J7196)

K "years." A "year" is used to represent the period of time an animal remains in an age-class and may not always represent a calendar year although it does in our fisheries example. There are $(l+1)$ distinguishable age-classes of animals ranging from 0 up to l (or more) yr of age. Each age-class moves forward one class each "year" except for the last one which includes all animals at least l yr of age. We further assume that each age-class has a different capture probability in the ith sample ($p_i^0, p_i^1, \ldots, p_i^l$) and a different survival probability from the ith to the $(i+1)$th sample ($\phi_i^0, \phi_i^1, \ldots, \phi_i^l$). Also immigration or emigration can occur for each age-class of the population, but births can only occur into the youngest (age 0) group. Thus, when referring to "survival," we really mean those animals which have not died or emigrated. Similarly, when referring to "recruitment," we really mean births and immigration for young animals (age = 0), but only immigration for the older animals (age > 0).

As well as the survival probabilities ($\phi_i^0, \phi_i^1, \ldots, \phi_i^l$) described above, the parameters to be estimated are the numbers of animals of each age-class in the population at each sampling time ($N_i^0, \ldots, N_i^l$), and the number of marked animals ($M_i^1, M_i^2, \ldots, M_i^{l+1}$), of each age-class from 1, 2, ..., $l+1$. The M_i^v parameters require further discussion. There are no marked young animals ($M_i^0 \equiv 0$) because after 1 "year" they will have moved into the next age-class (age = 1) and make up the M_i^1. We shall see that it is necessary to identify marked animals up to age $(l+1)(M_i^{l+1})$ to estimate the survival rate of the age l animals (ϕ_i^l) as these represent the survivors of the age l marked animals from the previous sample time $(i-1)$.

Assumptions and Notation

The age-dependent model we have described therefore has the following assumptions which are obvious extensions of those for the Jolly–Seber model (Seber 1973, p. 196).

i) Every animal in a particular age-class (v), whether marked or unmarked, has the same probability p_i^v of being captured in the ith sample provided it is alive and present in the population when the sample is taken.

ii) Every marked animal in a particular age-class (v) has the same probability (ϕ_i^v) of surviving from the ith to the $(i+1)$th sample and of still being in the study area at the $(i+1)$th sample provided it is alive and present in the population just after the ith sample.

iii) There is no mark loss during the study and all marks are reported on capture.

iv) All samples are instantaneous, i.e. sampling time is negligible and each release is made immediately after the sample.

v) All emigration from the population is permanent.

The following notation which is based on Seber (1973, p. 196) is used in this paper.

Parameters

M_i^v is the number of marked animals of age v in the population just before the ith sample ($v = 1, \ldots, l+1$; $M_i^0 \equiv 0$)

N_i^v is the number of animals of age v in the population just before the ith sample ($v = 0, 1, \ldots, l$)

ϕ_i^v is the probability that an animal of age v, alive at time i, survives until time $(i+1)$ ($v = 0, 1, \ldots, l$)

p_i^v is the probability that an animal of age v, alive at time i, is captured in the ith sample ($v = 0, 1, \ldots, l$)

Statistics

m_i^v is the number of marked animals of age v captured in the ith sample ($v = 1, \ldots, l$)

n_i^v is the number of animals of age v captured in the ith sample ($v = 0, 1, \ldots, l$)

R_i^v is the number of animals of age v released from the ith sample ($v = 0, 1, \ldots, l$). If there are "losses on capture" then R_i^v may be less than n_i^v

r_i^v is the number of the R_i^v which are captured again at least once after the ith sample ($v = 0, 1, \ldots, l$)

Z_i^v is the number of marked animals of age v caught before sample i, not caught at sample i, and caught again later ($v = 1, \ldots, l$)

T_i^v is the number of marked animals of age v which are caught at sample i or after sample i ($v = 1, \ldots, l+1$). This quantity is most easily obtained from previously defined statistics as $T_i^v = r_{i-1}^{v-1} + Z_{i-1}^{v-1}$ for $v = 1, \ldots, l+1$. Also $T_i^v = M_i^v + Z_i^v$ for $v = 1, \ldots, l-1$ and $T_i^l + T_i^{l+1} = M_i^l + Z_i^l$

Parameter Estimation

The maximum likelihood estimators of the parameters were originally derived in Pollock (1981b). Here we present approximately unbiased modifications of these maximum likelihood estimators using a similar approach to Seber (1973, p. 204).

Marked population sizes — The modified maximum likelihood estimators are given by the following equations.

$$\tilde{M}_i^v = m_i^v + \frac{Z_i^v (R_i^v + 1)}{(r_i^v + 1)} \quad \text{for } v = 1, 2, \ldots, l-1$$

$$\tilde{M}_i^l + \tilde{M}_i^{l+1} = m_i^l + \frac{Z_i^l (R_i^l + 1)}{(r_i^l + 1)}$$

$$\tilde{M}_i^l = \frac{T_i^l}{T_i^l + T_i^{l+1}} (\tilde{M}_i^l + \tilde{M}_i^{l+1})$$

$$\tilde{M}_i^{l+1} = \frac{T_i^{l+1}}{T_i^l + T_i^{l+1}} (\tilde{M}_i^l + \tilde{M}_i^{l+1}).$$

All the estimators are defined only for $i = 2, \ldots, K-1$, that is from the second to the next to the last sampling period.

Total population sizes — The modified maximum likelihood estimators are given by the following equations.

$$\tilde{N}_i^v = \frac{(n_i^v + 1)\tilde{M}_i^v}{(m_i^v + 1)} \quad \text{for } v = 1, 2, \ldots, l-1$$

$$\tilde{N}_i^l = \frac{(n_i^l + 1)(\tilde{M}_i^l + \tilde{M}_i^{l+1})}{(m_i^l + 1)}.$$

Notice that it is not possible to estimate N_i^0 because there are no marked animals of age 0. All the estimators are defined only for $i = 2, \ldots, K-1$, that is from the second to the next to the last sampling period.

Survival rates — The modified maximum likelihood estimators are given by the following equations.

$$\tilde{\phi}_1^v = \frac{\tilde{M}_2^{v+1}}{R_1^v} \text{ for } v = 0, 1, \ldots, l$$

$$\tilde{\phi}_i^v = \frac{\tilde{M}_{i+1}^{v+1}}{\tilde{M}_i^v - m_i^v + R_i^v} \text{ for } v = 0, 1, \ldots, l-1$$

$$\tilde{\phi}_i^l = \frac{\tilde{M}_{i+1}^{l+1}}{\tilde{M}_i^l + \tilde{M}_i^{l+1} - m_i^l + R_i^l}$$

It should be emphasized that $\hat{M}_i^v$ is the original maximum likelihood estimator and $\tilde{M}_i^v$ is the modified maximum likelihood estimator. Notice the need to estimate M_{i+1}^{l+1} to be able to estimate ϕ_i^l as discussed earlier. Also notice that all estimators are defined only for $i = 1, \ldots, K-2$, that is from the first to the next to the last survival period.

In some applications the fisheries biologist has only marked returns available from sport or commercial fishing. With no information on marked to unmarked ratios population sizes are no longer estimable but marked population sizes and survival rates can still be estimated as above.

Approximate variances and covariances of all the estimators are given by Pollock (1981b) and will not be presented here.

Testing Between Models

It is important to be able to test if survival and capture rates are different between age-categories. Pollock (1981b) showed that this is possible using a series of contingency table χ^2 tests based on the statistics shown below.

For the first $(K-1)$ samples we have $2 \times (l+1)$ contingency tables of the following form:

Age-class	Recaptured after sample i	Not recaptured after sample i	Animals released in sample i
0	r_i^0	$R_i^0 - r_i^0$	R_i^0
1	r_i^1	$R_i^1 - r_i^1$	R_i^1
.	.	.	.
.	.	.	.
.	.	.	.
l	r_i^l	$R_i^l - r_i^l$	R_i^l
Overall	r_i	$R_i - r_i$	R_i

Each table gives rise to an approximate χ^2 statistic with l degrees of freedom (Steel and Torre 1980, p. 495). In effect we are comparing the recapture rates of the $(l+1)$ different age-classes of animals and thus are testing that both survival and capture probabilities are independent of age.

For samples 2 to $K-1$ we have a series of additional $2 \times l$ contingency tables.

Age-class	Captured in sample i	Not captured in sample i	Marked animals captured in or after i
1	m_i^1	$T_i^1 - m_i^1$	T_i^1
2	m_i^2	$T_i^2 - m_i^2$	T_i^2
.	.	.	.
.	.	.	.
.	.	.	.
l	m_i^l	$T_i^l + T_i^{l+1} - m_i^l$	$T_i^l + T_i^{l+1}$
Overall	m_i	$T_i - m_i$	T_i

Note that there are no marked animals of age 0, and that this series of tables is only used if there are more than two age-classes. Each table gives rise to an approximate χ^2 statistic with $(l-1)$ degrees of freedom. Actually we are comparing the capture rates of known groups of marked animals of each age-class and thus are testing that capture probabilities are independent of age, whether survival is age-dependent or not.

As these χ^2 statistics are conditionally independent of each other we can obtain an overall χ^2 test statistic with $l(K-1) + (l-1)(K-2)$ degrees of freedom by adding the individual χ^2 statistics. In some cases it may be necessary to pool some cells in the tables in which case the degrees of freedom will be reduced (Steel and Torrie 1980, p. 474).

A Fisheries Example of Age-Dependent Survival

Biological Background

Here we illustrate the methodology with a mark–recapture study on northern pike carried out by (Mann 1980) on a 20 km section of the River Frome (2.285 ha in area), Dorset, England, between the winters of 1971–72 and 1978–79. Electrofishing was carried out each winter between November and March. Each fish was individually identified by attaching a numbered, metal tag to the maxilla. Tag loss was estimated to be ~9.5% per year (SE 2.7%).

In this analysis we just consider if a fish was captured at least once or not captured during a winter season. Also we divide the fish into just two age-categories because of the small numbers of older fish which were marked. The first age-class ($v = 0$) are fish of age 1 yr and the second age-class ($v = 1$) are fish of age at least 2 yr. Young-of-the-year fish could not be marked using the metal tags and are not considered in this analysis.

As electrofishing is size-selective we would expect older fish to have higher capture rates. It also might be expected that older fish have higher survival rates. Therefore this data set should be a useful illustration of when the age-dependent mark–recapture model should be used.

TABLE 1. Basic statistics used in the calculation of the age-dependent mark–recapture estimates.

Year	i	R_i^{0b}	r_i^0	T_i^{1c}	R_i^{1b}	r_i^1	T_i^{2c}	m_i^1	Z_i^1
1971–72	1	20	6	—	29	10	—	—	—
1972–73	2	29	4	6	22	5	10	12	4
1973–74	3	21	3	4	28	11	9	11	2
1974–75	4	29	4	3	24	5	13	14	2
1975–76	5	11	3	4	25	8	7	9	2
1976–77	6	47	13	3	31	11	10	11	2
1977–78[a]	7	22	4	13	38	3	13	24	2

[a]1978–79 was just a recapture year. No new animals were marked.
[b]There were no "losses on capture" so that $n_i^0 = R_i^0$ and $n_i^1 = R_i^1$.
[c]Recall that $T_i^v = r_{i-1}^{v-1} + Z_{i-1}^{v-1}$ for $v = 1$ and 2. Also recall that $T_i^1 + T_i^2 = m_i^1 + Z_i^1$.

TABLE 2. Approximately unbiased estimates of the marked and total population sizes with their standard errors in parentheses.

		Marked population sizes			Total population size, Age 2 or more
Year	i	Age 2 (M_i^1)	Age 3 or more (M_i^2)	Age 2 or more ($M_i^1 + M_i^2$)	(N_i^1)
1972–73	2	10.24 (4.1)	17.09 (6.3)	27.33 (9.4)	48 (17.7)
1973–74	3	4.87 (1.2)	10.96 (2.2)	15.83 (3.0)	38 (8.1)
1974–75	4	4.19 (1.7)	18.14 (5.4)	22.33 (6.5)	37 (11.3)
1975–76	5	5.37 (1.8)	9.41 (2.7)	14.78 (3.9)	38 (11.3)
1976–77	6	3.76 (1.2)	12.57 (2.7)	16.33 (3.4)	44 (9.5)
1977–78	7	21.75 (9.7)	21.75 (9.7)	43.50 (18.6)	68 (29.2)

POPULATION PARAMETER ESTIMATES

There were 295 fish captured in at least one of the 8 yr of the study. Each fish's capture history formed the basis of our analysis but is not presented here. The basic summary statistics necessary to calculate our estimates are given in Table 1 with the marked and total population size approximately unbiased estimates given in Table 2. Although we are interested in population sizes and survival rates for two age-classes of fish, recall that we will require information on a third age-class ($v = 2$, fish of age 3 or more) to complete the calculations. Also recall that it is not possible to estimate N_i^0, the population size of fish of age 1, because there are no marked fish of age 1 ($M_i^0 \equiv 0$).

This is a small population of fish and also notice that the estimates are not very precise. The precision of the estimates is best in the periods in the center of the study.

There is a lot of variability in the survival estimates again with those at the both ends of the chain, less precise than those in the middle (Table 3). However, notice that for every one of the six periods where estimates are possible the older fish have a higher survival rate. Therefore, despite the variability due to the small sample sizes this population shows strong evidence of age-dependent survival rates.

MODEL TESTING

In Table 4 we first tested the age-dependent survival and capture rates model versus the age-independent model (Jolly–Seber) using the contingency table approach described earlier. Note that the second test component (of equal catchability) cannot be performed as there are only two age-classes ($l = 1$). The overall χ^2 test statistic with 7 df is 6.99 which is not significant ($P = 0.45$).

This lack of significance surprised us considering the strong indication of age-dependent survival shown in Table 3. The problem is that the small sample sizes mean the test has low power. Therefore we compared the recovery rates of the age 1 fish (r_i^0/R_i^0) and the age 2 or more fish (r_i^1/R_i^1) on which the test is based. In all cases except the last ($i = 7$), the older fish have higher recovery rates. We computed the (binomial) probability of getting a result as extreme as six recovery rates out of seven being higher for the older fish if there was no age-dependence of survival and capture probabilities. This probability which is analogous to that of tossing six heads out of seven on a fair coin is 0.06. This casts serious doubt on the null hypothesis that survival and capture probabilities are independent of age. We conclude that the age-dependent model rather than the Jolly–Seber model should be used to analyze these data.

DISCUSSION

This population of pike shows strong evidence of age-dependence in the survival rates presented in Table 3. If we assumed that survival is not related to age the probability of obtaining our result of all six estimates being higher for the age 2+ fish is only 0.0156. We believe that this is an important result because mark–recapture models have not previously been used to document age-dependence of survival rates. We estimate the average annual survival rate to be 50% for the age 2+ pike and 34% for the age 1 pike.

In this study migration in and out of the study area is possible. Therefore by "survival" we really mean those fish

TABLE 3. Approximately unbiased estimates of the survival rate parameters and their standard errors in parentheses. Unadjusted and then adjusted for tag loss.

		Unadjusted estimates age of fish		Adjusted estimates age of fish	
Year	i	1[a]	2 or more[a]	1[b]	2 or more[b]
1971–72	1	0.51[c] (0.21)	0.59 (0.22)	0.56 (0.23)	0.65 (0.24)
1972–73	2	0.17 (0.04)	0.28 (0.09)	0.19 (0.04)	0.31 (0.10)
1973–74	3	0.20 (0.08)	0.55 (0.17)	0.22 (0.09)	0.61 (0.19)
1974–75	4	0.19 (0.06)	0.28 (0.10)	0.21 (0.07)	0.31 (0.11)
1975–76	5	0.34 (0.10)	0.39 (0.10)	0.38 (0.11)	0.43 (0.11)
1976–77	6	0.46 (0.20)	0.59 (0.27)	0.51 (0.22)	0.65 (0.30)
1977–78	7	—	—	—	—
Mean[d]		0.31 (0.05)	0.45 (0.07)	0.34 (0.06)	0.50 (0.08)

[a]These estimates are from the age-dependent model.
[b]These estimates are adjusted for a 9.5% annual tag loss. The standard errors are found using an approximation given in Pollock (1981b). Notice that the standard errors are slightly higher than for the unadjusted estimates.
[c]This survival rate is from year 1 to year 2.
[d]Arithmetic mean of yearly survival rates (unweighted).

TABLE 4. Testing for age-dependence of survival and capture rates.

	2 × 2 table			
Age 1 Age 2	r_i^0 r_i^1	$R_i^0 - r_i^0$ $R_i^1 - r_i^1$	χ_1^2 Statistics	r_i^{0*}/R_i^0 r_i^1/R_i^1
$i = 1$	6	14		0.30
	10	19	0.11	0.34
$i = 2$	4	25		0.14
	5	17	0.69	0.23
$i = 3$	3	18		0.14
	11	17	3.68	0.39
$i = 4$	4	25		0.14
	5	19	0.46	0.21
$i = 5$	3	8		0.27
	8	17	0.08	0.32
$i = 6$	13	34		0.28
	11	20	0.54	0.35
$i = 7$	4	18		0.18
	3	35	1.43	0.08

Overall test: $\chi_7^2 = 6.99$ ($P = 0.45$)

[a]The (binomial) probability of getting six recovery rates out of seven higher for the older fish is 0.06 if there is no age-dependence of survival and capture probabilities.

which have survived and remained in the area. In some fisheries studies (for example, a study in a closed lake) migration may not be possible and in those cases the estimates will only reflect the true survival rate assuming, of course, that the other model assumptions are reasonable.

There are two possible explanations for the age-dependence of the "survival" rates in this study. Mann (1980) felt that the younger pike were more likely to emigrate from the study area thus lowering the proportion remaining in the following year. Mann (1982) has also documented that younger pike suffer predation from the older pike.

It should be emphasized that the estimates obtained under this model will be less precise than those under the Jolly–Seber model. Therefore the age-dependent model should only be used when it is necessary. This was the case here where the model testing cast serious doubt on the validity of the Jolly–Seber model; our main purpose has been to demonstrate the age-dependence of the survival rates.

Planning Mark–Recapture Experiments

General Design Considerations

The need for careful planning of mark–recapture studies preferably involving joint collaboration between the biologist and a biometrician is of the utmost importance. Validity of model assumptions is crucial for any study and therefore we believe they should be considered critically at this preliminary stage while changes in the design are still possible. Perhaps more obvious is the need to consider the sampling effort required for adequate precision of the parameter estimates.

Assumptions

The marking scheme needs to be chosen very carefully. To use open population mark–recapture models we need to be able to establish the complete capture history of each fish handled. This requires a marking method which gives each fish its own unique mark. Batch marks do not give sufficient information. Mark (tag) loss should be minimized as it can cause serious negative bias on survival estimates although population size estimates are unaffected (in models that allow for both birth and death). Tag loss also causes a decrease in the precision of the estimates. If some tag loss is unavoidable, an attempt to estimate it should be made. Arnason and Mills (1981) have given an excellent account of tag loss problems (and solutions) from mark–recapture studies in fisheries. See also Seber and Felton (1981).

Survival rate estimates are based on ratios of different groups of marked animals and thus they strictly apply only to the marked subpopulation. When we assume that these rates apply to the whole population, we could have a serious

negative bias on the estimates if marking influences survival. The theory allows for "losses on capture" so any damaged fish should not be returned to the population. Sometimes fish are held in tanks to attempt to estimate the influence of marking on survival. Unfortunately the mortality observed in the artificial tank environment may not be the same as the mortality in the natural setting. There appears to be no ideal solution to this problem.

Heterogeneity of capture probabilities within an age-class can cause substantial negative bias on population size estimates whereas survival estimates although negatively biased are less affected. Carothers (1973) and Gilbert (1973) documented these results for the Jolly–Seber model using simulation, and their general conclusions also apply to the age-dependent model. Heterogeneity is very difficult to control in practice. It may be reduced by designing the study so that all sections of the study area are sampled with equal intensity. Sometimes (if samples are large enough) it may be possible to stratify on known sources of heterogeneity such as sex. There may also be a so-called "trap response" where marked fish in a particular age-class have a different probability of capture from unmarked fish in the same age-class. If marked fish are "trap shy," too few recaptures will be made and a positive bias on population size estimates results. On the other hand if marked fish are "trap happy," there will be too many recaptures, and a negative bias on population size estimates results. Survival rates are based only on the marked animals so that survival rate estimates are not influenced by "trap response." Therefore if a fisheries biologist is designing a study where survival estimation is of primary importance, he could use a mark–recapture method which had a trap response. If there is a "trap happy" response, higher precision on survival estimates results whereas a "trap shy" response reduces the precision. A design which attempts to minimize the influence of heterogeneity and trap response of the capture probabilities is presented later in this section.

Heterogeneity of survival probabilities within an age-class may also occur in natural populations of fish. This has little effect on estimates if an animal's survival probability is unrelated to its capture probability. This may be true in many mark–recapture studies where live capture is used and the animals are returned to the population. However, sometimes recapture is from fishermen turning in tags from their catch. Here an animal's survival probability is inversely related to its capture probability, and a negative bias on survival estimates can result (Pollock and Raveling 1982). The converse situation of a direct relationship between survival and capture rates could arise as a result of a common dependence on age or size. The age-dependent model described earlier and use of more than one sampling method (to reduce size selectivity) could alleviate this problem.

Precision

Now let us consider the question of precision of our parameter estimates. Clearly the obvious way to increase precision is to increase the capture rates for each age-class. Studies where the capture rates are less than 10–20% are unlikely to provide reasonable precision in small-to-moderate size populations. We realize that some fisheries studies may not be able to have high enough capture rates at a reasonable cost. Precision is influenced by many factors. In a particular study survival rate estimates are usually relatively more precise than population size estimates. Also if capture rates are roughly constant, then the estimates in the middle of the study are much more precise than those at either end. Precision is also influenced by the population sizes and survival rates. If we fixed the same capture rate precision would be higher in larger populations and for species with higher survival rates.

Arnason and Baniuk (1978) and Arnason et al. (1982) provide simulation programs for the age-independent Jolly–Seber model. Using "guesstimates" of the various parameters, biologists could find these programs very helpful in planning their experiments. No program presently exists for the age-dependent model but as mentioned earlier, estimates will have lower precision than under the Jolly–Seber model.

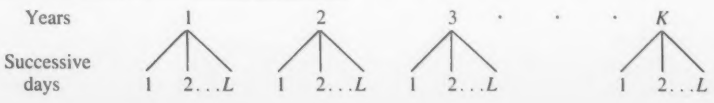
Manly (1971) found that studies with low capture probabilities also suffer from a problem in estimation of the variances of our point estimates. An underestimate of a parameter appears to be more precise than it really is. This is because the variance formulae involve the unknown parameters and we obtain an estimate of the variance by substituting parameter estimates for the true parameters in these equations.

It should also be emphasized that estimates of parameters such as the average survival rate for an age-class during the whole study have much higher precision than the individual survival rate estimates especially if the study continues for many periods. Sometimes these averages may be extremely important; as for example, in the testing of a general hypothesis that survival is age-dependent.

A Robust Design

The age-dependent model described in this paper had only one capture period each year or, if there were more it only used the information on whether the animal was captured or not in that year. This means that it is not possible to estimate the population size of the youngest age-class of animals (N_t^0) although it is possible to estimate their survival rate (ϕ_t^0). We now suggest a design which allows estimation of the N_t^0, increases precision, and also allows population size estimation to be robust to unequal catchability (heterogeneity or "trap response") of animals within an age-class.

Description — Let us consider the following representation of a mark–recapture experiment with K primary sampling periods (for example, years) and within each are L secondary sampling periods which are close to each other in time (for example, L successive days of captures):



We assume that the fisheries biologist is interested in the same parameters as before, the population sizes for each age-class (N_1^v, N_2^v, ..., N_k^v $v = 0, 1, 2, \ldots l$) and the survival rates for each age-class (ϕ_1^v, ϕ_2^v, ..., ϕ_{k-1}^v $v = 0, 1, 2, \ldots, l$). We also assume that the secondary periods are close enough together to be able to take the population as closed for those L periods.

Estimation procedure — A two-stage estimation procedure is possible. Survival rate estimation which is not influenced by "trap response" and is little influenced by heterogeneity of capture probabilities within an age-class could use the age-dependent model developed earlier in the paper on data pooled within each year. Here, by pooled we mean that we only consider if an animal is captured or not in each year.

Population size estimation for each age-class in each year could use a closed population model based only on the captures and recaptures of that age-class within that year. Traditionally fisheries biologists have used the Schnabel or Schumacher–Eschmeyer estimates for closed populations (Ricker 1975, p. 95). These estimates depend, however, on the assumption that all animals in a particular age-class are equally catchable. Recently there has been a lot of statistical research on closed population models which allow for heterogeneity and trap response of capture probabilities. We recommend that fisheries biologists consider use of these models which are described for biologists by Otis et al. (1978) and White et al. (1982). There is a comprehensive computer program "CAPTURE" available which makes use of the models quite practical.

A simpler version of this design is suggested by Pollock (1982) for the age-independent case. We believe that it may be extremely useful for some studies. Here it has the additional advantage that it allows estimation of the young animals population sizes (N_i^0) which are not estimable under the method given in the Section on The Age-Dependent Model.

Acknowledgments

We are grateful to Larry Crowder and two referees for their many helpful comments on an earlier draft of this manuscript.

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Age at Sexual Maturity in Icelandic Stocks of Atlantic Salmon (*Salmo salar*)

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SCARNECCHIA, D. L. 1983. Age at sexual maturity in Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 40: 1456–1468.

For Icelandic stocks of Atlantic salmon (*Salmo salar*) in 77 rivers, the combination of June ocean temperature, length of river ascended by the salmon, discharge of the river in July–September, and latitude explained much of the variation in percentages of grilse — 72% for females and 62% for males. For both sexes, percentage of grilse was directly related to ocean temperature but inversely related to length of river, discharge of river, and latitude. For stocks in 23 Southwest Coast rivers, length of river explained 72% of the variation in percentage of females that were grilse. Females in stocks south of the thermal gradients separating Atlantic from Arctic or Polar water tended to return as grilse; females north of the gradients tended to return after more than one winter at sea. The decline in percentages of grilse clockwise from southwestern to northeastern rivers corresponded closely with the decline in June ocean temperatures between these areas. I hypothesize that the salmon stocks have adapted their age at sexual maturity to the length and discharge of the rivers, natural mortality rates during their second year at sea, and average expected ocean temperatures, reflecting conditions for growth and survival, that the smolts encounter. Age at maturity appears not to be a direct causal response to any of these physical factors, and appears best understood only with reference to the entire life history pattern of each stock.

SCARNECCHIA, D. L. 1983. Age at sexual maturity in Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 40: 1456–1468.

Pour la plupart des stocks islandais de saumons atlantiques (*Salmo salar*) dans 77 rivières, une combinaison des facteurs suivants : température de l'océan en juin, longueur de la rivière remontée par le saumon, débit de la rivière en juillet–septembre et latitude expliquent une bonne partie de la variation du pourcentage de castillons — 72 % pour les femelles et 62 % pour les mâles. Chez les deux sexes, le pourcentage de castillons est en relation directe avec la température de l'océan mais en relation inverse avec la longueur de la rivière, son débit et la latitude. Dans le cas de stocks de 23 rivières de la côte méridionale, on peut relier à la longueur de la rivière 72 % de la variation du pourcentage de femelles castillons. Les femelles dans les stocks situés au sud des gradients de température séparant l'eau atlantique de l'eau arctique ou polaire tendent à retourner en rivière comme castillons; au nord de ces gradients, les femelles ont tendance à retourner en rivière après plus d'un hiver en mer. La diminution des pourcentages de castillons depuis les rivières du sud-ouest dans le sens des aiguilles d'une montre vers le nord-est correspond étroitement à l'abaissement des températures océaniques de juin de cette région à l'autre. J'émets l'hypothèse que les stocks de saumons ont adapté leur âge de maturité sexuelle à la longueur et au débit des rivières, au taux de mortalité naturelle durant leur deuxième année en mer et aux températures océaniques moyennes anticipées, reflétant les conditions, pour la croissance et la survie, que rencontrent les smolts. L'âge de la maturité ne semble pas être une réponse directe à aucun de ces facteurs physiques, mais s'expliquerait le mieux en fonction seulement des caractéristiques du cycle de vie entier de chaque stock.

Received November 9, 1982
Accepted June 2, 1983

Reçu le 9 novembre 1982
Accepté le 2 juin 1983

Printed in Canada (J7114)
Imprimé au Canada (J7114)

Printed in Canada (J7114)
Imprimé au Canada (J7114)

IN some Icelandic stocks of Atlantic salmon (*Salmo salar*), most fish return to their natal rivers after spending one winter in the sea;[1] in other stocks most fish return after two or more winters at sea. Similar variations are observed around the world between stocks of salmon inhabiting different rivers or different portions of the same river (Rounsefell 1958; Ricker 1972; Gardner 1976). Biologists have long sought the causes of these variations in life history. Dahl (1916) observed that northern Norwegian rivers had more large, older salmon and southern rivers had more small, younger salmon. Because, as a rule, salmon from the northern rivers spent more years in both freshwater and in the sea than did those of southern rivers, he speculated that "the whole life cycle of the salmon requires a longer period of development in the north than in the south."

More recently, Schaffer and Elson (1975) found significant positive correlations between mean weight of salmon, which indicated how long they had been at sea, and the length of the river that the salmon ascended for Canadian rivers in the Bay of Chaleur, the North Shore of the Gulf of St. Lawrence, and Nova Scotia. They argued that salmon required more energy to ascend longer rivers, and because of these energy requirements, selection would favor fish that stayed longer in the sea. They concluded that the observed relations beween length of river and mean weight of salmon were adaptive.

For salmon stocks in Quebec, Newfoundland, and Labrador, Power (1981) found a positive relation between discharge of river and the number of years a salmon from that river remained in the sea before maturing. He also stressed the adaptive nature of observed variations in age at maturity.

Why do most salmon in some Icelandic stocks return to their rivers after 1 yr at sea but most salmon in other stocks return after 2 or more yr at sea? This question relates to variations between stocks and their underlying causes. The answer to this question is sought by biologists who want to explain variations in life history patterns, by anglers who want to know why they catch mostly big salmon in one river and small salmon in another, by commerical fisherman who get different prices per unit weight for salmon of different sizes, and by aquaculturists and salmon ranchers who want to manipulate return rates of younger and older salmon for maximum profit.

If the observed variations in age at maturity are primarily adaptive, some long-term environmental factors must be inducing these adaptations. The problem is to separate the environmental factors that have led to adaptations by fish of particular stocks from the factors that merely produce short-term physiological responses by individual fish. Assuming sufficient nondominance genetic variability on which selection can act, differences in environments between stocks will lead to adaptive variations, especially if the environmental differences persist over time.

To attempt to determine which environmental factors may have led to adaptations in age at maturity in Iceland's stocks of salmon, I investigated the correlation between percentage of male grilse and female grilse in the salmon catch of 77 rivers and four factors: the length of the river ascended by the salmon; the discharge of the river when the adult salmon migrate upstream (July–September); the latitude of the river; and ocean temperature when the smolts enter the ocean (June–August).

Methods

SALMON LIFE HISTORY DATA

Salmon ascend about 80 rivers in Iceland and most of these rivers support carefully managed angling with rods (Gudjónsson 1978). River owners and fishing clubs keep accurate statistics on weight (at intervals of 0.5 kg) and sex of individual salmon caught. There is no significant fishery for salmon in the ocean by Icelanders and my preliminary analysis indicates that, unlike some North American stocks (Paloheimo and Elson 1974), slight or no changes in age composition have occurred in most stocks over the last 20 yr. Harvesting with fishing rods is less size selective than harvesting with gill nets, and because of the significant cost of permits, anglers keep most fish they catch regardless of the fish's weight.

For 76 rivers I determined the number of years the salmon had spent at sea by analyzing weight-frequencies of rod-caught salmon separately by sex. For one other river, Thjorsá (No. 73 in Fig. 1), which is a large glacial river fished mainly by gill nets, I used weight–frequency data of gill-netted salmon of known sex. In most stocks, most females weighing more than 3.5 kg and most males over 4 kg had spent 2 or more years at sea. For selected stocks, I analyzed scales to verify ages of females of 3.0–3.5 kg and males of 3.5–4.0 kg weight ranges within which grilse and multi-sea-winter salmon often overlapped. To lessen the possibility of changes in age composition over time biasing the data, I calculated where possible the average percentage of grilse in the catch for a constant period of several years, usually 1967–73. For rivers where few salmon were caught or the data were not separated by sex over all years, I used whatever data were available for any years before 1974. The effects of introduced hatchery fish on stock composition were small during this pre-1974 period. The final statistics I obtained from these calculations were the average percentages (over several years) of males that were grilse (hereafter called percent male grilse) and the percentages of females that were grilse (hereafter called percent female grilse).

LENGTH AND DISCHARGE OF RIVERS

Rivers in Iceland were classified by Rist (1956) as glacial (J), direct runoff (D), spring-fed (L), and lake-fed (S), and each type has distinct discharge characteristics. Glacial rivers, e.g. upper tributaries of Blanda (No. 49) and Thjorsá (No. 73), are typically brownish to whitish, at least in summer, because of fine sediments in the water. Many large rivers receiving glacial water have clear water tributaries (such as Blanda's tributary Svartá, No. 50), in which adult salmon spawn and young salmon rear. The discharge of glacial rivers is typically highest in July and August because the glaciers are then melting rapidly (Rist 1956). Because

[1]In this paper, salmon that have matured or are about to mature after one winter in the sea (having one ocean annulus) are called grilse; salmon with two or more ocean annuli are called multi-sea-winter salmon.

TABLE 1. Summary of percent male and female grilse, ascendable length, discharge, latitude, and offshore ocean temperatures for 77 Icelandic rivers classified by type according to Rist (1969). (J = glacial, D = direct runoff, L = spring-fed, S = lake-fed; types listed in combinations in order of decreasing importance.

River	Type	Male grilse (% of all males)	Female grilse (% of all females)	Length of river (km)	Discharge of river (m^3/s)	Latitude (minutes N of 63°N)	Ocean temperature (°C)
1 Ellidaár	L+S+D	91	86	6	2.9	67	8.05
2 Úlfarsá	S+D+L	95	91	7	1.1	68	8.05
3 Leirvogsá	D+L	87	84	8	1.9	72	8.05
4 Laxá í Kjós	D+S	74	67	18	4.8	78	8.05
5 Bugda	D+S	81	81	4	1.2	79	8.05
6 Brynjudalsá	D	91	85	10	1.0	81	8.05
7 Laxá í Lsveit	D+S	77	72	13	1.5	85	8.05
8 Leirá	D	92	94	4	0.4	84	8.05
9 Andakílsá	D+S	87	81	5	7.2	93	8.05
10 Hvítá	D+L+J	73	66	48	80.6	101	8.05
11 Grímsá/Tunguá	D+S	81	75	32	4.7	94	8.05
12 Flókadalsá	D	91	88	30	3.1	96	8.05
13 Reykjadalsá	D+L	77	77	47	1.8	99	8.05
14 Thverá	D	69	50	60	3.2	105	8.05
15 Nordurá	D	75	59	45	17.2	106	8.05
16 Gljúfurá	D	96	93	20	0.4	102	8.05
17 Langá	D+S	88	80	17	8.5	97	6.93
18 Álftá	L+D	82	66	10	2.4	97	6.93
19 Hítará	S+D	70	64	14	6.5	104	6.93
20 Haffjardará	L+D+S	72	54	16	5.1	110	6.93
21 Straumfjardará	D+S	68	49	11	2.3	110	6.93
22 Fródá	D+L	75	69	5	0.4	113	6.93
23 Laxá á Skógst	D	75	67	3	0.5	121	6.93
24 Hördudalsá	D	83	66	10	1.0	120	6.93
25 Midá í Dölum	D	78	65	12	2.3	120	6.93
26 Haukadalsá	D+S	72	57	6	4.4	123	6.93
27 Fáskrúd	D	77	64	8	1.4	132	6.93
28 Flekkudalsá	D	85	72	4	1.0	129	6.93
29 Krossá á Skardsst	D	85	74	5	1.5	136	6.81
30 Hvolsá/Stadarh	D	84	74	8	1.3	143	6.81
31 Laugardalsá	D+S	79	50	3	0.4	179	5.81
32 Ísafjardará	D	74	51	4	1.2	166	5.81
33 Langadalsá	D	57	26	20	1.6	170	5.81
34 Hvannadalsá	D	62	41	5	0.7	174	5.81
35 Selá, Stfirdi	D	80	37	12	2.2	170	5.09
36 Vídidalsá, Stfirdi	D	70	31	3	0.8	160	5.09
37 Hrófá	D	69	34	2	0.5	158	5.09
38 Vikurá	D	45	30	7	0.6	146	5.09
39 Bakkaá	D	64	29	5	0.4	138	5.09
40 Laxá á Hrútafirdi	D	57	45	2	0.5	134	5.09
41 Hrútafjardará/Siká	D	59	29	10	1.9	127	5.09
42 Midfjardará	D	60	31	33	4.0	133	5.09
43 Núpsá	D	64	32	33	0.5	128	5.09
44 Austurá	D	53	25	24	1.1	129	5.09
45 Vesturá	D	64	34	32	1.5	130	5.09
46 Vídidalsá/Fitjaá	D+S	50	19	45	10.0	142	5.09
47 Vatnsdalsá	D+L+S	54	35	43	6.4	149	5.09
48 Laxá á Ásum	S+D	80	61	15	2.3	157	5.09
49 Blanda	D+J	33	18	100	56.2	140	5.09
50 Svartá	D	57	25	41	5.9	149	5.09
51 Laxá-Ytri	D	69	47	15	6.0	163	5.09
52 Fossá í Laxárdal	D	70	21	2	1.1	177	4.44
53 Sæmundará	D	60	6	28	1.1	158	4.44
54 Húseyjarkvísl	D+L	56	31	27	8.6	158	4.44
55 Hofsá í Vesturdal	D+J	61	25	2	4.0	174	4.44
56 Fljótaá	S+D	74	34	7	6.4	182	4.44
57 Fnjóská	D	50	20	34	32.7	169	4.44
58 Skjálfandafljót	D+L+J	69	15	28	88.3	171	4.44
59 Laxá í Adaldal	L+S	41	17	27	49.2	174	4.44

TABLE 1. (*Concluded*)

River	Type	Male grilse (% of all males)	Female grilse (% of all females)	Length of river (km)	Discharge of river (m^3/s)	Latitude (minutes N of 63°N)	Ocean temperature (°C)
60 Ormarsá	D+L	45	35	7	9.2	203	3.26
61 Deildará	D+S	47	38	6	0.4	205	3.26
62 Svalbardsá	D	49	24	13	15.7	191	2.97
63 Sandá	D+L	54	22	10	11.5	190	2.97
64 Hölkná	D	42	34	10	10.3	189	2.97
65 Hafralónsá	D	37	20	25	9.0	185	2.97
66 Midfjardará/Kverká	D	65	21	5	13.3	181	3.36
67 Selá í Vopnafirdi	D+L	64	36	7	12.2	170	3.36
68 Vesturdalsá	D	68	43	28	0.9	161	3.36
69 Hofsá	D	70	21	31	5.9	158	3.36
70 Breiddalsá	D	90	72	10	6.9	108	2.98
71 Geirlandsá	D	71	71	5	4.1	50	8.22
72 Eldvatn	L	89	86	10	31.0	37	8.22
73 Thjórsá	D+J+L	41	27	48	428.0	56	8.46
74 Stóra-Laxá	D	56	21	96	6.6	65	8.46
75 Bruará	L+S	68	7	72	60.6	70	8.46
76 Sogid	L+S	71	61	39	102.0	63	8.46
77 Hvitá	D+J+S+L	70	33	95	120.7	65	8.46

upstream migration of salmon is from June to August, fish migrating up glacial rivers to spawn in clear-water tributaries do so when discharge from the rivers is near the annual peak.

Direct runoff rivers (e.g. Nordurá, No. 15, and Hofsá, No. 69) are formed by the confluence of smaller streams. Because of water-tight bedrock, the discharge of these rivers depends on season and weather, and tends to be high in early spring or summer when snowmelt is greatest. In most of the best direct runoff rivers of salmon, discharge usually peaks before June and is low by July when salmon begin their migration upstream. Because direct runoff rivers are frequently small as well, salmon ascending these rivers usually are confronted with much lower discharges than are those ascending rivers fed by glaciers.

Spring-fed rivers (e.g. tributaries of Bruará, No. 75, and Sogid, No. 76) frequently originate in gushing springs located beneath younger parts of the Móberg Formation. The flows of the springs and the rivers fed by them are stable. Salmon ascending either large or small spring-fed or lake-fed rivers encounter stable, predictable flows. In general, Iceland's largest rivers in their main stems are combinations of the four types. For example, the main stem of Blanda is of two types and Thjorsá is of three types.

For one-third of the rivers, the Icelandic National Energy Authority Hydrological Survey operates gauging stations that measure mean daily discharge. Rist and Sigurdsson (1981) summarized the average monthly discharges at these gauging stations over periods from 1 to 48 yr, depending on the river. For these rivers, I estimated mean discharge from July to September by averaging the monthly mean discharges for these months.

For another one-third of the rivers, only spot measurements of discharge were available during the 3-mo period (Rist 1967, 1968). If more than one estimate existed, these estimates were averaged to get the best available estimate of mean discharge.

For the last one-third of the rivers, there were no direct discharge measurements. For these rivers, I estimated the average discharge during July–September by assuming that discharge per square kilometre of drainage area (Rist 1969) for rivers of unknown discharge was the same as that for neighboring rivers of known discharge and of the same or similar combination type according to Rist's (1956) classification (Table 1).

For each river I determined the maximum distance that salmon ascended before their migration was blocked by waterfalls or other physical or thermal obstructions. This information came from data compiled by Einar Hannesson of the Iceland Institute of Freshwater Fisheries and from my own surveys of about 10 rivers. For most rivers, the distance that the salmon ascended was precisely known (Table 1).

LATITUDE AND OCEAN TEMPERATURE

I estimated the latitude of each of 77 rivers (Geodetic Institute Maps of Iceland, Scale 1:100 000) as being midway between the mouth of the river and the uppermost point where salmon were known to ascend (Table 1).

Along the submarine ridge connecting Scotland and Greenland on which Iceland is located, a strong thermal gradient exists between Eystrahorn and Vestrahorn, between the warmer, more saline (>35‰) water of the North Atlantic and the colder, less saline (<35‰) water of the Iceland Sea (Thomsen 1938; Stefánsson 1962; Fig. 1). Off northwestern Iceland, along the Iceland–Greenland part of the ridge, there is another abrupt thermal gradient where warm North Atlantic water (the Irminger Current) meets the cold water of the Iceland Sea and the East Greenland Current (Stefánsson 1962). This gradient extends east to 66°N 26°W and then stretches northeastward. Between this gradient and the northwestern peninsula of Iceland, the Irminger Current penetrates northward and eastward throughout summer. The water temperature at a 20-m depth may be one Celsius degree lower off Kögur than off Latrabjarg. East of Kögur the ocean temperatures from June to August vary greatly between years. In warmer years the North Icelandic winter water stratifies

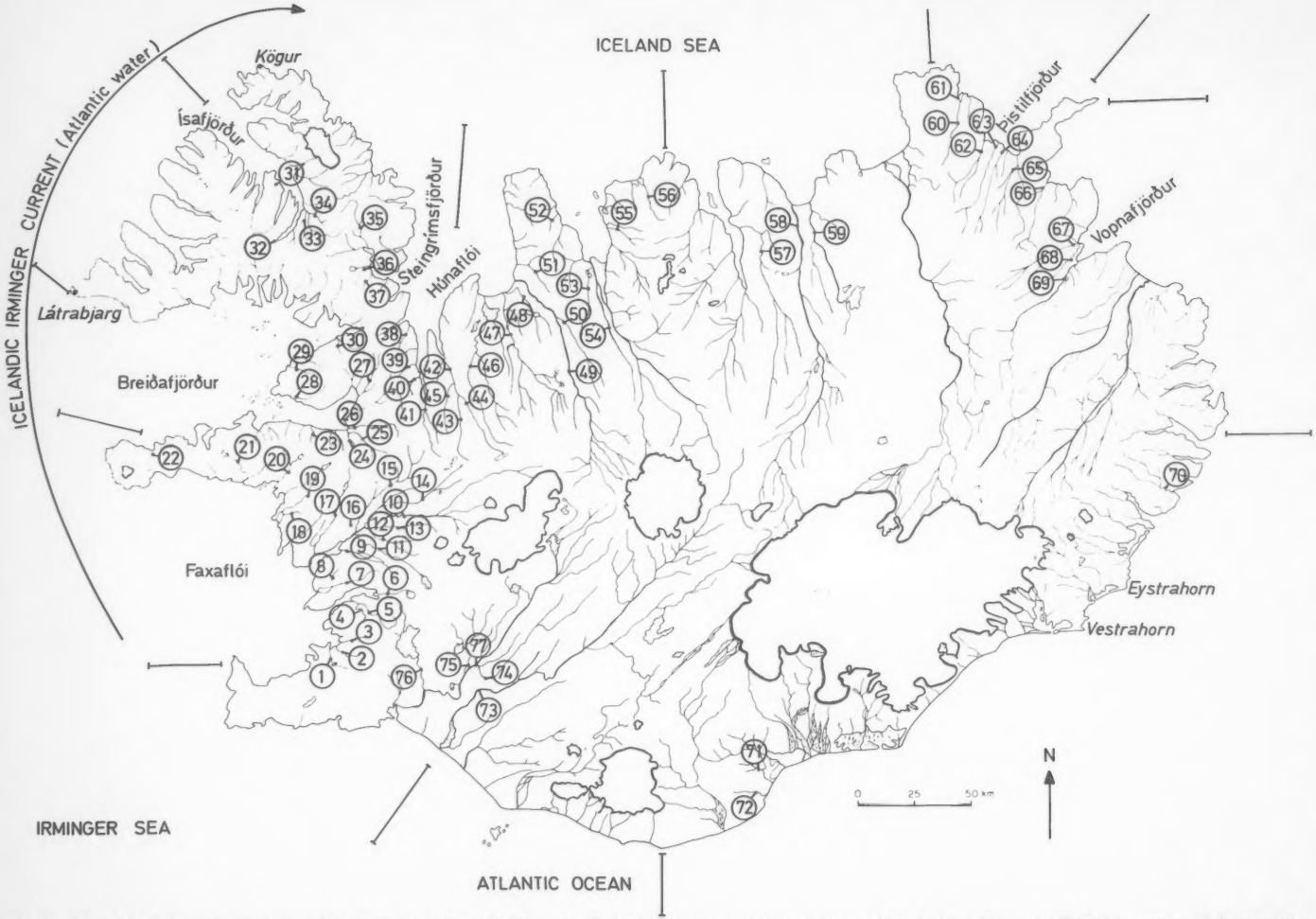

FIG. 1. Map showing 77 major and minor salmon rivers and geographical features of Iceland. Ocean temperature transects are shown by black lines. See Table 1 for names and characteristics of the rivers.

TABLE 2. Variation in percentages of male and female grilse explained by stepwise regression of ocean temperature and length, discharge, and latitude for 77 Icelandic rivers. (**$P < 0.01$; *$P < 0.05$.)

Sex of grilse, and variable	Additional % explained by adding this variable to model	% of total variation explained
Males		
Ocean temperature	34**	34**
Length of river	21**	54**
Discharge of river	6**	60**
Latitude	2*	62**
Percent grilse = 3.9201 (ocean temperature) − 0.2659 (length) − 0.7862×10^{-1} (discharge) − 0.1006 (latitude) + 65.3585.		
Females		
Ocean temperature	43**	43**
Length of river	24**	67**
Discharge of river	3**	70**
Latitude	2**	72**
Percent grilse = 6.5955 (ocean temperature) − 0.5044 (length) − 0.9225×10^{-1} (discharge) − 0.2033 (latitude) + 47.4314.		

and dominates the surface layer; in colder years a layer of cold Polar water (<34‰ salinity) overlies the North Icelandic winter water (Malmberg 1972). Salmon smolts leaving southern and western rivers in June would thus swim into warm (6−9°C at 20 m) saline Atlantic water, whereas smolts leaving northern and northeastern rivers would swim into cool north Icelandic winter water mixed with penetrating Atlantic water. During cold years the smolts would swim into a surface layer of cold Polar water (<2°C at 20 m).

Ocean temperatures off Iceland have been measured at several depths for many years at standard stations along standard transects by the Marine Research Institute, Reykjavík. For 12 transects around the coast (Fig. 1), I combined the June temperatures at 20- and 25-m depths over the first four stations and averaged these values for each transect over a 33-yr period (1946−78). Because data were unavailable for many transects and years, I had only from 2 to 24 temperatures from which to calculate mean long-term June temperatures. Fortunately, the data along the more variable north coast were more nearly complete (data for 8−24 yr along each transect) than those along the much less variable south coast (data for 2−7 yr). Consequently the resulting mean relationships between transects for long-term June temperatures agreed closely with Stefánsson's (1960) regional 1950−60 mean estimates at 20 m. There were too few data to be analyzed for July and August, but because average surface water temperatures in July and August are closely related to temperatures in June (Stefánsson 1969, fig. 1), I had excellent evidence that June temperature relationships between transects at 20 m were maintained through August. I assigned each river a value for June ocean temperature based on where it entered the sea in relation to the 12 transects and on Stefánsson's (1960) charts of temperatures at a 20-m depth from 1950 to 1959. Each river was assigned 1 of 12 ocean temperatures (Table 1).[2]

[2]More detailed data used to calculate mean values for percentages of grilse, discharge of rivers, and ocean temperatures are available from the author.

I chose the 20-m depth because salmon are believed to feed near the surface (Stasko et al. 1973). Although the 20-m depth is within the surface layer, the temperature does not fluctuate as much as that at the surface in response to sudden changes in weather.

STATISTICAL ANALYSES

I investigated relations between percent of grilse (males and females separately as dependent variables) and length of river, discharge of river, latitude, and ocean temperature (independent variables) with linear, multiple, and stepwise regression analyses. I also computed partial correlation coefficients to assess the effect of one independent variable while controlling for the effect of one or more other variables (Nie et al. 1975).

Results

VARIATIONS IN PERCENT GRILSE

For female salmon, the combination of ocean temperature, length of river, discharge of river, and latitude explained 72% of the variation in percentage of grilse. All four independent variables made a significant contribution to explaining this variation (F-test, $P < 0.01$; Table 2). Individually, percentage of grilse was directly related to ocean temperature ($r = 0.66$; $P < 0.01$), inversely related to length of river ($r = -0.34$; $P < 0.01$) and latitude ($r = -0.60$; $P < 0.01$), but not significantly related to discharge ($r = -0.18$; $P > 0.05$). Ocean temperature and length of river, which were the first two variables to enter the stepwise model, explained 67% of the variation in percentage of grilse; discharge and latitude explained an additional 5%.

Ocean temperature and latitude were closely correlated with each other, but overall the correlations between independent variables were weak, even though some were statistically significant (Fig. 4).

Combinations of variables were much better than any individual variable at explaining the variation in duration of sea

TABLE 3. Partial correlation coefficients for independent variables and percentages of male and female grilse for 77 Icelandic rivers (all significant at $P < 0.01$ level).

For a given:	The variable	Explained − % of the variation in % of male grilse	Explained − % of the variation in % of female grilse
Latitude	Length of river	31	42
Ocean temperature	Length of river	31	41
Lat. + ocean temp.	Length of river	33	45
Length of river	Ocean temperature	49	62
Discharge of river	Ocean temperature	45	52
Length + discharge	Ocean temperature	54	65
Latitude	Discharge of river	23	20
Ocean temperature	Discharge of river	22	18
Lat. + ocean temp.	Discharge of river	24	20
Length of river	Latitude	44	58
Discharge of river	Latitude	40	47
Length + discharge	Latitude	51	62

TABLE 4. Variation in percent of male and female grilse explained by stepwise model of length, discharge, and latitude for 23 Icelandic Southwest Coast rivers (Nos. 1−16, 71−77). (**$P < 0.01$; *$P < 0.05$.)

Sex of grilse, and variable	Additional % explained by adding this variable to model	% of total variation explained
Males		
Discharge of river	48**	48**
Length of river	21**	69**
Latitude	1	70**
Females		
Length of river	72**	72**
Latitude	6**	78**
Discharge of river	3	81**

TABLE 5. Variation in percent of male and female grilse explained by stepwise regression model of length, discharge, and latitude for 25 Icelandic North Coast rivers (Nos. 35−59). (**$P < 0.01$; *$P < 0.05$.)

Sex of grilse, and variable	Additional % explained by adding this variable to model	% of total variation variation
Males		
Length of river	39*	39**
Latitude	3	42**
Discharge of river	2	44**
Females		
Discharge of river	20*	20*
Length of river	2	22
Latitude	1	23

residence. For example, for a given length and discharge, ocean temperature explained 65% of the variation in percentage of grilse. Similarly, for a given latitude and ocean temperature, length of river explained 45% of the variation in percentage of grilse (Table 3).

For the males, ocean temperature, length of river, discharge of river, and latitude explained 62% of the variation in percentage of grilse. All four variables entered the model significantly (F-test, $P < 0.05$; Table 2). Percentage of male grilse was directly related to ocean temperature ($r = 0.58$; $P < 0.01$), but inversely related to length of river ($r = -0.32$; $P < 0.01$), discharge of river ($r = -0.26$; $P < 0.05$) and latitude ($r = -0.52$; $P < 0.01$). For a given length and discharge of river, ocean temperature explained 54% of the variation in percentage of grilse; for a given ocean temperature and latitude, length of river explained 33% of the variation (Table 3).

For both females and males the best two-variable combina-

tion for explaining percentage of grilse was ocean temperature and length of river (Table 2).

For Southwest Coast rivers (Nos. 1–16 and 71–77) considered separately, length of river explained 72% of the variation in percent of female grilse (Fig. 5). Latitude explained an additional 6% and discharge 3% for 81% of the total variation. For males, length and discharge together accounted for 69% of the variation in percentage of grilse (Table 4).

For North Coast rivers (Nos. 35–59) considered separately, the relations between length, discharge, and percentage of grilse were less close. For males, only length entered the stepwise model significantly, explaining 39% of the variation in percentage of grilse. For the females, discharge was the first variable entered and was the only variable closely related to percent of grilse (Table 5).

Other Results

In 75 of 77 rivers the percent of grilse was lower for females than males. For southwest coast rivers (Nos. 1–9) flowing into Faxaflói, percentages of both male and female grilse generally exceeded 80, whereas salmon returning to many northern and northeastern rivers (e.g. Sæmundará, No. 53; Skjálfandafljót, No. 58; Hofsá, No. 69) were mostly grilse males and multi-winter sea females (Table 1).

As the regression analyses indicated, along the north coast the percentage of female grilse corresponded closely with oceanic temperatures off the rivers in summer. For example, for short rivers (<20 km, encircled in Fig. 2 and 3), representations of grilse dropped from 64 to 74% for the eight rivers (Nos. 22–25, 27–30) flowing into Breidafjördur (temperature 6.9°C) to 41 to 51% for the three short rivers (Nos. 31, 32, 34) in Ísafjördur (temperature 5.8°C), and to 29 to 45% for six rivers (Nos. 35–41) in western Húnaflói (temperature 5.1°C). For northeastern rivers (Nos. 60–64, 66, 67) for which temperatures were even lower (3.0–3.4°C), only 21 to 38% of the salmon were grilse. The drop in grilse from 64 to 74% in Breidafjördur to less than 50% in Ísafjördur and Húnaflói coincided closely with the position of the Iceland–Greenland Ridge and declining ocean temperatures between Breidafjördur and Húnaflói (Fig. 1, 2). Salmon in Breiddalsá (No. 70), which is 60 km north of the eastern thermal gradient, were mostly grilse. Unfortunately, there were too few salmon stocks in eastern Iceland to locate the point where the stocks again changed from mostly multi-sea-winter salmon to mainly grilse.

Although ocean temperature and latitude were closely correlated, there was clear evidence that ocean temperature off northwestern Iceland rather than latitude was affecting the percentages of grilse. In three short rivers in Ísafjördur (Nos. 31, 32, 34; temperature 5.8°C), the percentages of grilse were 41, 50, and 51, but in three rivers in Steingrímsfjördur (Nos. 35–37, temperature 5.1°C), which are farther south and originate near the same mountainous area, the percentages of grilse were 31, 34, and 37. Similarly, the salmon in rivers 27–30 in Breidafjördur (temperature 6.8°C) were 64–74% grilse but those in rivers 35–41 flowing into western Hunaflói (temperature 5.1°C) which are at a latitude similar to that of rivers in Breidafjördur were only 29–45% grilse (Fig. 2).

The long glacial rivers had lower percentages of female grilse than did surrounding, short nonglacial rivers. For example, Blanda (No. 49) and Skjálfandafljót (No. 58) each had fewer than 20% grilse. Svartá (No. 50), the large freshwater tributary of Blanda, had a higher percentage of grilse than Blanda as a whole.

The effects of river length and discharge were most clearly seen in the long, large rivers in the southwest (Nos. 73–77), which had a much lower percentage of female grilse than neighboring shorter, smaller volume rivers (Fig. 2). The northern rivers Fnjoská and Laxá (Nos. 57 and 59), which were both over 25 km long and had high discharges, also had low percentages of grilse (Fig. 1, 2).

The relations between ocean temperature, length, discharge and latitude, and grilse were not as well defined for males as for females, but most results for males agreed with results for females. The decline in percent of grilse from Breidafjördur to Vopnafjördur is evident in Fig. 3.

Discussion

In Iceland's stocks of Atlantic salmon, length of river, discharge of river, latitude, and ocean temperature are strongly correlated with, and appear to influence, the salmon's age at maturity. According to Schaffer's (1974, 1979) model, salmon from long, fast rivers should tend to remain in the sea longer than would those from short, easy rivers (Schaffer and Elson 1975). Because length and discharge are imperfect indicators of the work ($\int F \cdot dl$) a fish must do to reach its spawning grounds and to spawn, Schaffer and Elson suggested that long, large rivers would favor larger fish with greater energy reserves. That is, their increased size and fecundity would more than compensate for their extra year's mortality because their larger size would facilitate successful upstream migration and spawning. My analysis of Rist's unpublished data indicated that velocities generally increased with increasing discharge, which would further explain why large salmon might have an advantage in ascending larger, longer rivers. Ísaksson (1981) reported that most hatchery-reared salmon from Dalsá, an upper tributary of the long river Hvitá (No. 77), matured after 2 yr at sea, whereas most smolts of similar size from Kollafjördur hatchery stock reared under similar conditions returned as grilse. Ísaksson's results confirm the genetic tendency toward late maturation in an Icelandic salmon stock from a long river.

However, the Icelandic data and other published and unpublished information do not indicate that late age at maturity is necessarily an adaptive trait evolved by salmon in response to greater energy requirements for migration and spawning in long, large rivers. If such an adaptation existed, more large salmon should spawn in the upper parts of long rivers and more small salmon should spawn in the lower parts of rivers. The data do not support this expectation for either Atlantic or Pacific salmon. Killick and Clemens (1963) reported that most sockeye salmon (*Oncorhynchus nerka*) of the Fraser River's many discrete stocks returned after 2 yr at sea, but three-sea-winter salmon were most abundant compared to two-sea-winter fish in lower river stocks such as in Pitt and Harrison rivers, rather than in upper river stocks such as the Stuart River. Yet, Stuart River fish traveled over 1000 km

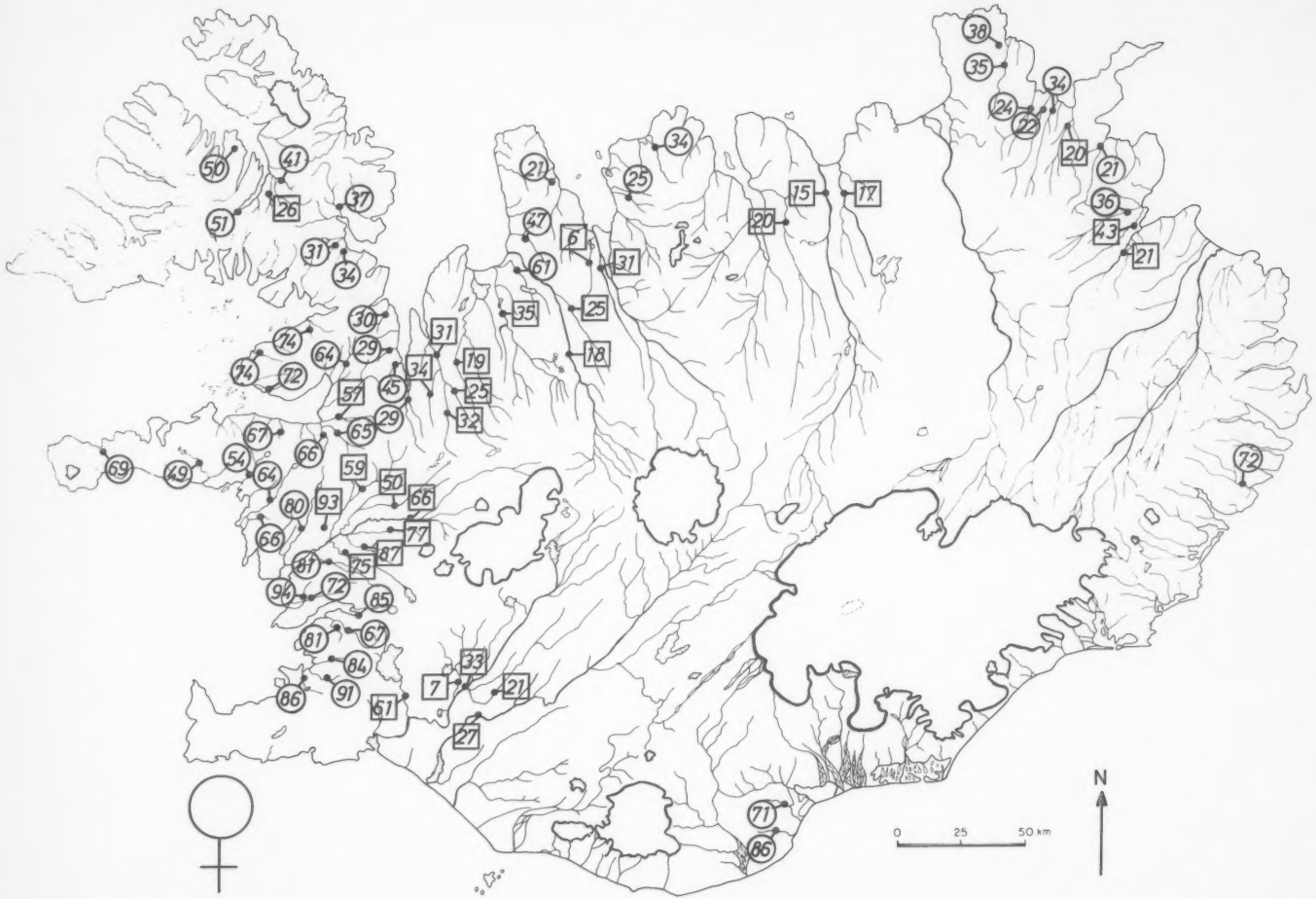

FIG. 2. Percent females that were grilse in the catch of 77 Icelandic rivers; squares: >20 km ascendable length; circles: <20 km ascendable length.

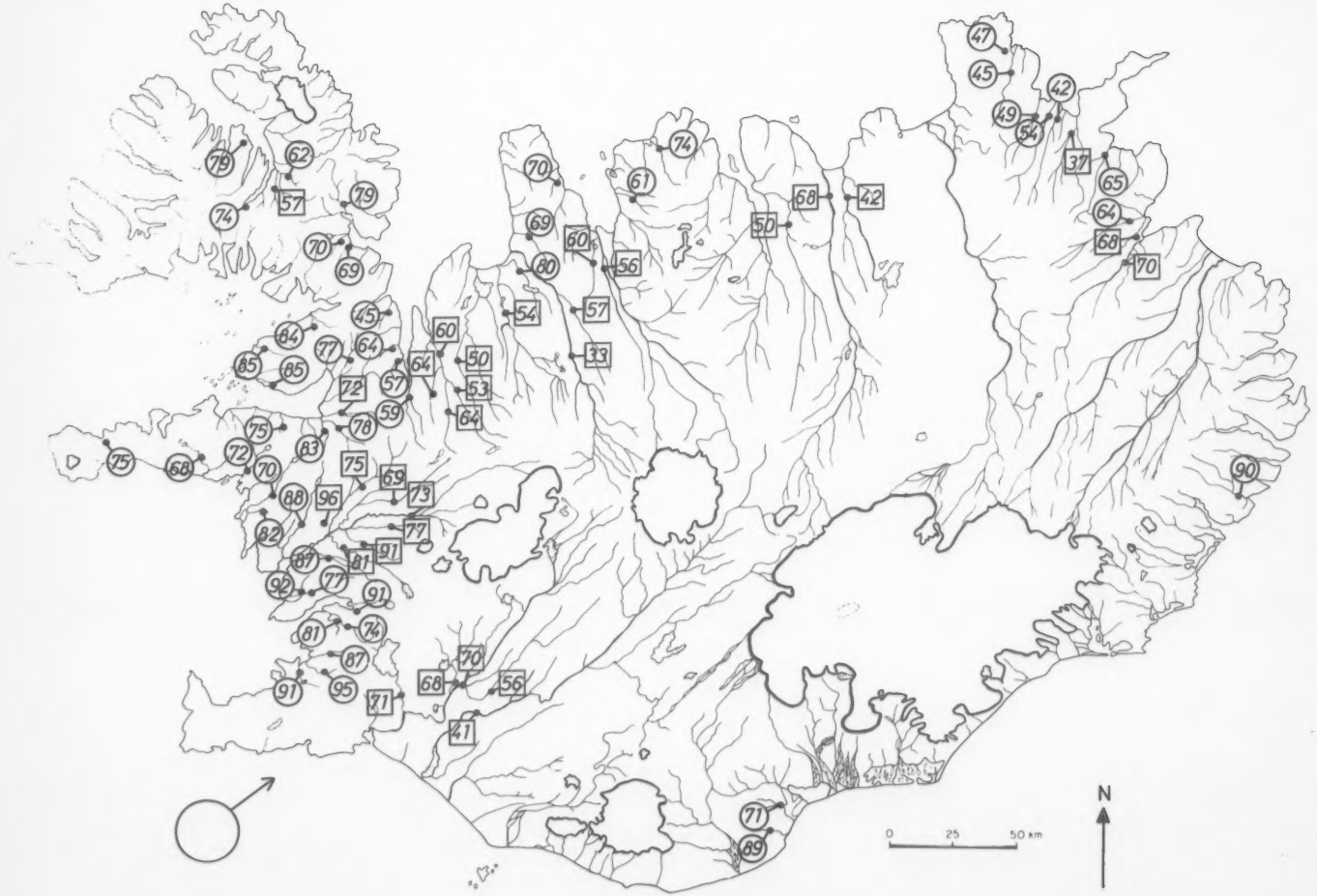

FIG. 3. Percent males that were grilse in the catch of 77 Icelandic rivers; squares: >20 km ascendable length; circles: <20 km ascendable length.

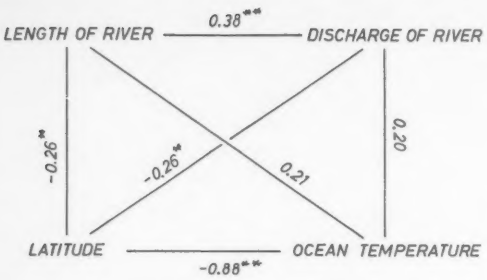

FIG. 4. Correlations between length of river, discharge of river, latitude, and offshore ocean temperature for 77 Icelandic rivers (*$P < 0.05$; **$P < 0.01$).

upstream to spawn, 10 times as far as the Pitt River fish and 10 times the length of the longest ascendable Icelandic river. If large size and late age at maturity were adaptive responses to energy requirements for ascending the river, the upper Fraser stocks should, contrary to observations, have more large, older fish than the lower river stocks. In Iceland, female Atlantic salmon caught in the lower part of Thverá in 1967 and 1968 were 68% grilse, mid-river catches were 69% grilse, and upper river catches in Litla Thverá were 74% grilse (Institute of Freshwater Fisheries, unpublished data). In Scotland, the largest salmon in the River Tweed appear to spawn in the main channel, not in the upper tributaries (D. Mills, letter to author, December 15, 1982). In the River Tana between Norway and Finland, the largest salmon also appear to spawn in the lower main channel (A. Rikstad, letter to author, April 5, 1983). These two observational results cast even more doubt on Schaffer and Elson's hypothesis, despite its intuitive appeal.

Idler and Clemens (1959) and Gilhousen (1980) performed detailed analyses of energy expenditures for Fraser River sockeye and found that males from the Adams River, which migrated 480 km upstream, were maturing at sea and apparently ceased feeding earlier than fish from the Stuart River, which continued feeding until they entered the river. Such differences in maturation schedules indicate the danger of a particular life history trait such as age at maturity can be viewed as an isolated response to one or two environmental factors. Life history traits interact. Age at maturity is best viewed only in the context of the entire life history of the organism (Warren and Liss 1980).

Perhaps age at maturity is not itself the adaptive trait. Rather, perhaps there exist adaptively advantageous stock-specific weights and physiological conditions females and males should attain, and the observed variations in age at maturity are merely indications of how many years it takes fish of each stock to reach this state. How would such an adaptive response explain the lower percentages of grilse in the north than in the south and the decreasing percentages of grilse from Breidafjördur to Vopnafjördur?

Smolts from the northwest may grow faster in the the ocean than those in the northeast because there is more warm Atlantic water in the west and perhaps more accompanying planktonic invertebrates and larval fish. If salmon stocks have

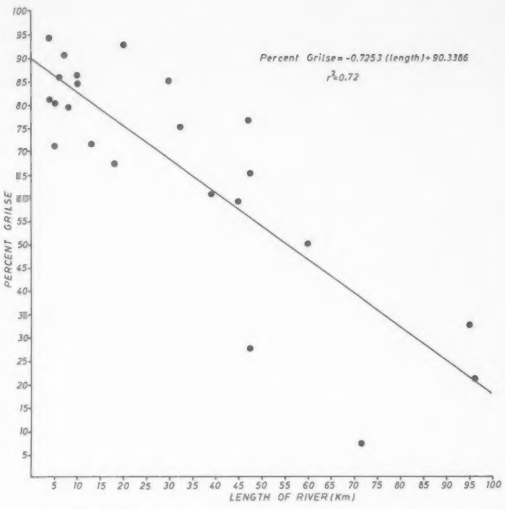

FIG. 5. Relation between length of 23 South Coast salmon rivers and percentage of females in the catch that were grilse.

evolved adaptively advantageous weights (and resultant fecundities) at which to mature under their unique environmental conditions and mortality rates, they may reach this weight (and resultant fecundity) after 1 yr at sea more often in the northwest than in the northeast, and more often in the south and west than in the northeast and northwest. This result would explain the strong correlations between sea temperature and percentages of grilse. It may also be advantageous for a smolt in the north to delay seaward migration until later in the season, when higher oceanic water temperatures and better feeding conditions may permit faster growth and better survival.

Smolts from northern stocks may emigrate later than those of southern stocks not only because of ocean conditions but because of slower warming of northern rivers and resulting later smoltification. In general, relative coastal air temperatures in spring and summer decrease from southwest to northeast around Iceland, parallel to sea temperatures (unpublished data, Icelandic Meteorological Office).

There have been few studies of smolts in Iceland, but most smolts from Ellidaár (No. 1) migrate into warm Atlantic water (8°C at 25 m) in late May and early June (Poe 1975). Preliminary results from some northern rivers show that salmon parr are silvery as late as September (S. Einarsson, personal communication). If salmon in the north and south spawn at about the same time, northern stocks would have fewer productive spring and summer months in the sea for active growth than southern stocks from when they left the river until they spawned. Because growth in weight and fecundity increase faster than linearly (Pope et al. 1961), there would still be strong selection within a year's growing season for reaching a large size (especially for courtship in males) and a large fecundity (especially for females). More large salmon that had reached this adaptively advantageous weight

would mature (Alm 1959), but smaller fish would tend to remain in the sea. Fewer salmon in the northeast would attain this weight than in the northwest, and far fewer than in the south.

Similarly, perhaps the long, large rivers in the south have smolts which emigrate from the lower river in summer or autumn as well as in spring. Such a migration would explain the delayed maturity in these rivers. Although early warming of rivers may produce faster growth and earlier smoltification, in the end, the timing of the smolt migration must be a physiological response to short-term environmental conditions (e.g. weather, immediate food supply) superimposed upon an adaptive response to long-term environmental conditions (e.g. climate, food production cycles).

Although length, discharge, latitude, and ocean temperatures have been clearly correlated with age at maturity in Icelandic salmon, much more information is needed on smolt size, timing of smolt migrations, migration and feeding areas at sea, and maturation schedules both at sea and in the rivers before we clearly understand how these four factors affect age at sexual maturity.

Also according to Schaffer's (1974) model, high mortality during the second year at sea should favor fish returning as grilse, whereas high growth rates during the second year at sea should favor fish returning as multi-sea-winter salmon. If natural mortality during the second year at sea is less in the north than in the south, for a given fecundity, more fish would delay maturation in the north than in the south. Unfortunately, there is as yet no information on mortality rates of Icelandic salmon stocks.

I was better able to explain variations in percent of female grilse than male grilse because male parr mature in many rivers. In a river with many such parr, there would appear to be a higher proportion of multi-sea-winter salmon than actually exists. As no mature female parr have been found in Iceland, the percentages of grilse are more reliable for females than for males.

A higher percentage of male grilse than female grilse is found in nearly all rivers because it is probably less important for a male than for a female to have a high fecundity. Even mature male parr have abundant sperm and compete with large males during spawning (Jones and King 1949). Apparently male salmonids have more flexibility in their responses to age at maturity because of their lower reproductive investment (lower weight of sperm; Jonsson 1977).

Within a region, salmon from long, large, Icelandic rivers probably will show greater genetic tendencies toward late maturity than salmon from short, small rivers, as Ísaksson (1982) found for salmon in Dalsá. It is unclear if the differences in age at maturity between northern and southern stocks inhabiting short, small rivers have a strong genetic basis or if individual fish will readily alter their age at maturity physiologically under new environmental conditions imposed by fish breeders. Well-controlled breeding and rearing experiments should clarify in which cases genetic or environmental influences are dominant.

Acknowledgments

I thank Thorsteinn Sæmundsson of the Icelandic Fulbright Committee for encouraging my research in Iceland. My special thanks to Thór Gudjónsson, Director of the Institute of Freshwater Fisheries, and Árni Ísaksson, for encouraging and supporting this research. Jón Kristjánsson, Einar Hannesson, Thórólfur Antonsson, Sigurdur Már Einarsson, and Sumarlidi Óskarsson helped me with various aspects of the study. Sigurjón Rist of the National Energy Authority Hydrologic Survey generously provided streamflow data and reviewed the manuscript. Svend-Aage Malmberg of the Hydrologic Section of the Marine Research Institute contributed the data on sea temperatures. Gunnar Hilmarsson gave me expert help with the computer analyses. I also thank Arnthór Gardarsson, R. J. Gibson, D. Mills, Kari Ranta-aho, and W. M. Schaffer for reviewing and criticizing the manuscript at various stages.

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Bioaccumulation and Effects of Cadmium and Zinc in a Lake Michigan Plankton Community

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MARSHALL, J. S., J. I. PARKER, D. L. MELLINGER, AND C. LEI. 1983. Bioaccumulation and effects of cadmium and zinc in a Lake Michigan plankton community. Can. J. Fish. Aquat. Sci. 40: 1469–1479.

We conducted four in situ experiments in the southern basin of Lake Michigan to determine the responses of the plankton community to additions of cadmium (3 μg/L) and zinc (15, 30, 60, and 90 μg/L) as well as the bioaccumulation of zinc by different species of crustacean zooplankton. Total cadmium and zinc concentrations in treated enclosures (accounting for pretreatment lakewater concentrations of ~20 ng Cd and ~1 μg Zn per litre) were calculated from measurements of ^{109}Cd and ^{65}Zn with known specific activities.

Zinc significantly reduced zooplankton populations and several other properties of community structure and function at concentrations much lower than those previously reported to be toxic to zooplankton and well below the levels established for protection of freshwater life. Zinc additions as low as 15 μg/L significantly reduced chlorophyll *a*, primary productivity, dissolved oxygen, specific zooplankton populations, zooplankton species diversity, and community similarity within 2 wk. Populations of several zooplankton species were severely reduced by 15 μg/L; for example, the population of the rotifer *Conochilus unicornis* was reduced to less than 1% of that in controls. Secondary, indirect effects included significant increases of a few populations, including *Bosmina longirostris* and *Keratella cochlearis*, for zinc additions of 15 and 30 μg/L. Most of the populations and community properties that we measured showed somewhat different percentage reductions in response to a given zinc addition at different times, but their relative (rank) values at different times were similar. Specific zooplankton populations were more sensitive to zinc than community similarity indices, and species diversity indices were relatively insensitive. Bioaccumulation of zinc by different species of crustaceans increased with added zinc but showed few significant differences among species. The small differences among species could, nevertheless, partially account for some of the observed changes in zooplankton community structure.

MARSHALL, J. S., J. I. PARKER, D. L. MELLINGER, AND C. LEI. 1983. Bioaccumulation and effects of cadmium and zinc in a Lake Michigan plankton community. Can. J. Fish. Aquat. Sci. 40: 1469–1479.

Nous avons mené quatre expériences *in situ* dans le bassin méridional du lac Michigan en vue de déterminer les réactions de la communauté planctonique à des additions de cadmium (3 μg/L) et de zinc (15, 30, 60 et 90 μg/L) ainsi que la bioaccumulation de zinc chez différentes espèces de crustacés planctoniques. Les concentrations totales de cadmium et de zinc dans des enceintes traitées (représentant des concentrations d'eau de lac d'avant-traitement de ~20 ng Cd et ~1 μg Zn/L) ont été déterminées à partir de mesures de ^{109}Cd et ^{65}Zn d'activités spécifiques connues. Le zinc réduit de façon significative les populations de zooplancton ainsi que plusieurs autres propriétés structurales et fonctionnelles de la communauté à des concentrations de beaucoup inférieures à celles mentionnées antérieurement comme étant toxiques pour le zooplancton et bien au-dessous des niveaux adoptés pour la protection des organismes d'eau douce. Des additions de zinc aussi faibles que

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Printed in Canada (J6614)
Imprimé au Canada (J6614)

15 μg/L réduisent de façon significative la chlorophylle *a*, la productivité primaire, l'oxygène dissous, les populations zooplanctoniques spécifiques, la diversité des espèces zooplanctoniques et la similitude de communauté en moins de deux semaines. Les populations de plusieurs espèces zooplanctoniques sont sérieusement réduites par additions de 15 μg/L; comme exemple, la population de rotifères *Conochilus unicornis* est réduite à moins de 1 % de celle des témoins. Parmi les effets indirects secondaires, on note d'importantes augmentations chez quelques populations, y compris celles de *Bosmina longirostris* et *Keratella cochlearis*, après additions de zinc de 15 et 30 μg/L. La plupart des propriétés de population et de communauté mesurées montrent des pourcentages de diminution quelque peu différents en réponse à une addition de zinc donnée et à des moments différents, mais leurs valeurs relatives (rang) demeurent les mêmes. Les populations zooplanctoniques spécifiques sont plus sensibles au zinc que les indices de similitude des communautés, alors que les indices de diversité des espèces sont relativement insensibles. La bioaccumulation de zinc par différentes espèces de crustacés augmente en fonction des additions de zinc, mais ne diffère pas significativement d'une espèce à l'autre. Ces faibles différences interspécifiques pourraient néanmoins expliquer certains changements observés dans la structure des communautés zooplanctoniques.

Received August 27, 1981
Accepted June 6, 1983

Reçu le 27 août 1981
Accepté le 6 juin 1983

CADMIUM and zinc rank among the most toxic of metals, especially to plankton. Cadmium is toxic to freshwater phytoplankton at 2–4 μg/L (Chiaudani and Vighi 1978; Conway 1978; DeNoyelles et al. 1980; Gachter 1976) and to zooplankton at 0.2–1.0 μg/L (Biesinger and Christensen 1972; Marshall 1978; Marshall and Mellinger 1980; Marshall et al. 1981c). Zinc is toxic to phytoplankton at 4–7 μg/L (Chiaudani and Vighi 1978; Gachter 1976), but has not been reported to be toxic to zooplankton at concentrations lower than 40–70 μg/L (Baudouin and Scoppa 1974; Biesinger and Christensen 1972). However, the lowest zinc concentrations previously reported to be toxic to zooplankton were based on laboratory studies of selected species and thus failed to include the more sensitive (difficult to culture) species that exist in natural plankton communities. These previous studies also failed to measure zinc bioaccumulation or to include important species interactions that can compound direct toxic effects (Marshall and Mellinger 1980). No previous study on zinc bioaccumulation and toxic effects in a natural zooplankton community has been reported.

The principal objectives of this study were to determine and evaluate (1) responses of the Lake Michigan phytoplankton and zooplankton communities to elevated concentrations of cadmium and zinc, (2) zinc bioaccumulation by different species of crustaceans in the Lake Michigan zooplankton community, and (3) the sensitivity and consistency of several indices of toxic stress. We studied zinc more extensively than cadmium because we had previously found that at the ambient Zn:Cd ratio in Lake Michigan, zinc strongly suppresses cadmium bioaccumulation and that the combined effects of cadmium and zinc are mainly due to zinc (Marshall et al. 1981a).

In this paper we show that zinc can significantly reduce zooplankton populations and several other properties of community structure and function at concentrations much lower than previously reported to be toxic to zooplankton and well below the levels established for protection of freshwater life. We also provide new insights into the role of metal bioaccumulation in changing community structure, the comparative behavior of different indices of toxic stress, and the usefulness of in situ experiments with natural plankton communities.

Methods

We conducted two 2-wk experiments in the southern basin of Lake Michigan to determine phytoplankton and zooplankton community responses to several levels of zinc. The first experiment also included one level of cadmium. Field procedures were generally the same as those described by Marshall and Mellinger (1980). Both experiments were conducted at a sampling station located ~32 km northeast of the Chicago Harbor.

We initiated the first dose–response experiment on July 10, 1980. Forty 18-L polyethylene carboys were filled with water collected from depths of 4–9 m. Eight carboys were treated with 30, eight with 60, and eight with 90 μg Zn/L. Eight other carboys were treated with an addition of 3 μg Cd/L, and eight were used as controls. Half of the control and treated replicates were filled, treated, and deployed in the morning; the other half were done in the afternoon. The zinc and cadmium added in the afternoon contained ~4 nCi (1 Ci = 37 GBq) ^{65}Zn/μg Zn and ~500 nCi ^{109}Cd/μg Cd as radioisotopic monitors for the added metals. We suspended the carboys at depths of 6–8 m from four buoys (10/buoy) and positioned them so that the average depth for controls and each treatment was the same (~7 m). After 2 wk, 31 carboys were found and retrieved. Dissolved oxygen was measured with a YSI model 57 oxygen meter, and 3 L of water were removed from each carboy for determinations of chlorophyll *a*, micronutrients, and primary productivity. Pheopigment-

TABLE 1. Average concentrations (± SE) of total zinc, total particulate zinc (>0.45 μm) and coarse particulate zinc (>54 μm) in control and Zn-treated enclosures after 2 wk in Lake Michigan, August 6–18, 1980. Numbers in parentheses indicate number of samples (enclosures).

Added Zn, μg/L	Total Zn, μg/L	Total particulate Zn, μg/L	Coarse particulate Zn, μg/L
0	1.0[a]	0.4±0.0 (2)	0.05±0.00 (8)
15	17.1±0.5 (2)	1.1±0.1 (2)	0.32±0.02 (8)
30	31.2±2.0 (2)	1.4±0.1 (2)	0.32±0.02 (8)
60	62.1±1.2 (2)	1.9±0.4 (2)	0.42±0.04 (8)
90	89.6±5.9 (2)	2.1±0.1 (2)	0.43±0.03 (8)

[a]Assumed concentration.

corrected chlorophyll *a* concentration was determined according to Strickland and Parsons (1972). Micronutrient concentrations (NO_3-N, NH_4-N, SiO_4-Si, and PO_4-P) and primary productivity were determined by autoanalysis and radiocarbon methods, respectively, as described by Parker et al. (1981). The remaining volume (15 L) was strained through a 54 μm-mesh filter funnel to remove the net plankton, which was carefully rinsed and preserved in 4% formalin. A 150-mL sample of each ^{109}Cd- or ^{65}Zn-labeled filtrate was passed through a 0.45-μm membrane filter to prepare samples for determinations of radioisotope concentrations in the 0.45- to 54-μm and <0.45-μm fractions. Radioisotope concentrations were determined by gamma-ray spectrometry using a NaI detector. Stable cadmium and zinc concentrations in Lake Michigan water (and in control enclosures) were ~20 ng Cd per litre (Muhlbaier and Tisue 1981) and ~1 μg Zn per litre (G. T. Tisue, Clemson University, personal communication). Quantitative zooplankton analyses and calculations of indices were done as described by Marshall and Mellinger (1980). Biomass for each category of crustaceans was calculated by multiplying the number per litre by an appropriate individual dry weight selected from the literature (see Hawkins and Evans 1979). After the radioisotope and zooplankton analyses were completed, each net plankton sample (>54-μm fraction) was collected on a preweighed, 28-μm-mesh Nitex disk (47 mm diameter), dried at 55°C, and reweighed to determine the dry weight (biomass) of the net plankton.

We initiated the second dose–response experiment on August 6, 1980 using the same methods as in the first, except for the addition of another level of zinc (15 μg/L) and deletion of the cadmium treatment. The zinc added to the 32 treated carboys contained 4 nCi ^{65}Zn/μg Zn, and carrier-free ^{65}Zn was added to the eight controls. All 40 carboys were retrieved after 2 wk, and samples were prepared for various determinations as described above.

We conducted two other 2-wk experiments in parallel with the two dose–response experiments to determine the bioaccumulation of zinc by different species of the crustacean zooplankton. We initiated the first experiment on July 10, 1980. Eight 18-L carboys were filled with subsamples of the same water used to fill the carboys for the dose–response experiment. Four were treated with a zinc addition of 30 μg/L, and four were used as controls. The added zinc contained ~185 nCi ^{65}Zn/μg Zn, and carrier-free ^{65}Zn (~5.6 μCi/L) was added to the controls. These carboys were suspended in the lake from two additional buoys. We retrieved

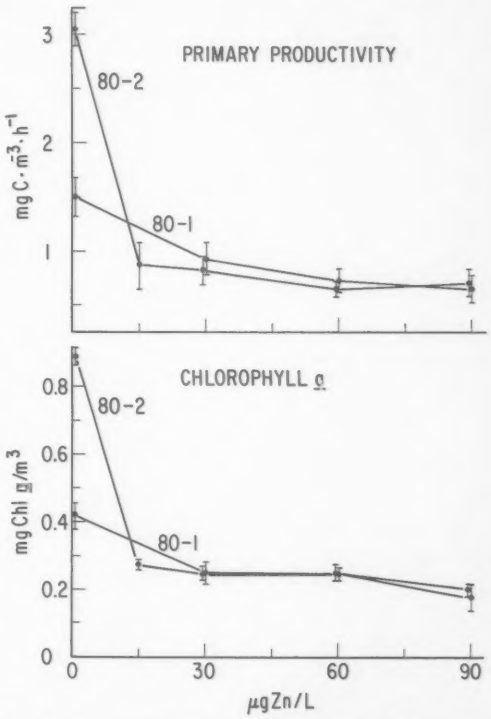

FIG. 1. Primary productivity (above) and chlorophyll *a* concentrations (below) in relation to added zinc concentrations in the water in first (80-1) and second (80-2) dose–response experiment.

all eight carboys after 2 wk, but the caps were loose on two. After retrieval, we strained the contents of the six securely capped carboys through a 243-μm-mesh filter funnel to retain the larger crustaceans. These animals were transferred through three baths of fresh lakewater and allowed to swim about each time for several seconds. The crustaceans from each carboy were then collected on a 47-mm diameter, 243-μm-mesh Nitex disk and stored at 4°C until the next day. We then sorted out subsamples (10–20 individuals each) of

TABLE 2. Average concentrations (±SE) of dissolved oxygen, NO_3-N, NH_4-N, SiO_4-Si, and PO_4-P in control and Cd- or Zn-treated enclosures after two 2-wk in situ experiments in Lake Michigan, July 10–23, 1980 (Experiment 1) and August 6–18, 1980 (Experiment 2). Numbers in parentheses indicate number of samples (enclosures). Underlined values are significantly different from controls ($P < 0.05$), as indicated by *t*-tests.

	Experiment 1					Experiment 2				
Solute	Controls (6)	3 µg Cd/L (5)	30 µg Zn/L (7)	60 µg Zn/L (6)	90 µg Zn/L (7)	Controls (8)	15 µg Zn/L (8)	30 µg Zn/L (8)	60 µg Zn/L (8)	90 µg Zn/L (8)
O_2, mg/L	8.7±0.1	8.3±0.1	8.4±0.1	8.4±0.1	8.5±0.1	7.5±0.1	7.1±0.1	7.0±0.1	7.0±0.1	7.1±0.1
NO_3-N, µmol/L	11.8±0.3	11.7±0.4	10.5±0.7	11.6±0.2	11.4±0.3	15.4±0.4	14.4±0.5	15.7±0.5	13.8±1.8	13.6±1.6
NH_4-N, µmol/L	2.8±0.2	3.4±0.2	3.5±0.8	3.1±0.4	3.0±0.2	2.3±0.4	2.5±0.5	3.2±0.7	2.6±1.0	2.6±0.7
SiO_4-Si, µmol/L	11.6±0.2	12.5±0.5	12.9±0.3	13.4±0.1	12.5±0.5	3.0±0.4	4.2±0.4	3.7±0.2	3.7±0.2	3.5±0.2
PO_4-P, µmol/L	0.01±0.01	0.04±0.01	0.01±0.01	0.02±0.01	0.03±0.01	0.07±0.01	0.05±0.01	0.09±0.02	0.12±0.03	0.06±0.01

adult calanoid or cyclopoid copepods, several species of cladocerans, and mixtures of crustaceans. These were placed on preweighed Al pans, dried at 55°C, and reweighed with a Cahn electrobalance to determine their dry weights. Concentrations of ^{65}Zn were measured, and zinc bioaccumulation (µg Zn/g dry weight) were calculated from the measured concentrations of ^{65}Zn and its specific activity.

We initiated the second bioaccumulation experiment on August 6, 1980. Duplicate carboys for each of three levels of added zinc (15, 30, and 60 µg/L) and controls were prepared and incubated in the lake in parallel with the second dose–response experiment. All eight carboys were retrieved after 2 wk, and samples of the larger crustaceans were removed and carefully rinsed as in the first experiment. Each sample was preserved in $CaCO_3$-neutralized, 4% formalin for ~4 h until it was returned to the laboratory, where it was then collected on a 47-mm diameter, 243-µm-mesh screen and kept moist overnight in a refrigerator. The next day the samples were sorted and prepared for determinations of dry weight and zinc bioaccumulation as in the first experiment.

Results

Total zinc concentrations in the water in treated enclosures after 2 wk (Table 1) show that very little of the added zinc was sorbed by the container walls. Concentrations of coarse and total particulate zinc (Table 1) indicate that net plankton and total seston sorbed only 1 and 4%, respectively, of the total zinc in the Zn-treated carboys.

The effects of zinc on primary productivity and chlorophyll *a* were quite similar in both experiments (Fig. 1). Primary productivity and chlorophyll *a* were significantly reduced by added zinc concentrations as low as 30 µg/L in the first experiment ($P < 0.05$) and 15 µg/L in the second ($P < 0.01$). Little or no further reduction resulted from additions of >30 µg/L. In Cd-treated carboys (first experiment) average primary productivity (0.71 ± 0.06 mg $C \cdot m^{-3} \cdot h^{-1}$) and chlorophyll *a* concentration (0.25 ± 0.02 mg/m^3) were both significantly reduced ($P < 0.05$). The average concentration of SiO_4-Si was significantly increased by zinc in the first experiment, and dissolved oxygen was significantly reduced by each metal treatment in both experiments (Table 2).

The cadmium and zinc treatments also caused significant changes in the average population densities of several species of crustaceans (Table 3) and rotifers (Table 4) and the average values of several indices of community similarity and species diversity (Table 5). A few of the crustaceans and rotifers exhibited significant increases or decreases (or both) with increasing zinc concentration (Fig. 2). The increase shown by *Keratella crassa* at 15 µg/L was not significant, but the decrease at 90 µg/L was (Table 4).

Average values of *PS* (a community similarity index) for the crustacean zooplankton community were significantly reduced by all treatments in both experiments (Table 5). Only one of the three species diversity indices (N_0) showed a significant decrease in the crustacean community in the first experiment, and none was significantly reduced by 15 µg per litre in the second (Table 5). In contrast to the crustacean community, the rotifer community showed significant reductions of both similarity indices and all three species diversity

TABLE 3. Average numbers per litre (±SE) of different categories of crustacean zooplankton in control and Cd- or Zn-treated enclosures for two in situ experiments conducted in Lake Michigan during July 10–23 (Experiment 1) and July 6–18 (Experiment 2). Numbers in parentheses indicate number of samples (enclosures). Underlined values are significantly different from controls ($P < 0.05$), as indicated by *t*-tests.

	Experiment 1					Experiment 2				
Category	Controls (6)	3 μg Cd/L (5)	30 μg Zn/L (7)	60 μg Zn/L (6)	90 μg Zn/L (7)	Controls (8)	15 μg Zn/L (8)	30 μg Zn/L (8)	60 μg Zn/L (8)	90 μg Zn/L (8)
Cladocera										
Daphnia retrocurva	0.4±0.2	0.04±0.02	0.2±0.1	0.02±0.02	0.03±0.02	0.8±0.2	0.5±0.1	0.2±0.01	0.01±0.01	0.02±0.01
D. galeata mendotae	8.4±2.5	7.7±3.5	2.5±0.6	1.3±0.7	0.4±0.1	6.1±0.6	5.0±0.5	5.4±0.5	1.6±0.2	0.3±0.2
Bosmina longirostris	19.8±2.6	4.0±0.5	3.6±0.7	1.2±0.3	1.6±0.8	2.3±0.9	4.1±1.4	6.5±1.6	1.7±0.3	0.2±0.1
Eubosmina coregoni	0.4±0.2	0.1±0.1	0.3±0.1	0	0.2±0.1	2.8±0.4	3.9±0.5	2.6±0.5	2.8±0.5	1.4±0.3
Holopedium gibberum	0	0	0	0	0	1.2±0.3	0.4±0.1	0.06±0.04	0	0
Total Cladocera	28.9±3.4	11.9±3.7	6.6±1.2	2.5±0.9	2.2±0.8	13.2±0.9	14.1±1.7	14.7±1.7	6.2±0.6	2.0±0.3
Copepoda										
Diaptomus minutus	1.2±0.1	1.0±0.1	1.2±0.1	1.1±0.3	1.1±0.1	1.0±0.2	0.7±0.1	0.8±0.1	0.8±0.1	0.8±0.1
D. ashlandi	4.0±0.9	1.8±0.4	3.4±0.6	2.5±0.4	2.6±0.5	0.04±0.02	0.04±0.02	0.01±0.01	0.01±0.01	0
D. oregonensis	0.03±0.02	0.02±0.02	0.06±0.04	0.03±0.02	0.07±0.04	0.5±0.1	0.5±0.2	0.3±0.1	0.1±0.03	0.1±0.03
D. sicilis	0.2±0.1	0.06±0.06	0.1±0.1	0.02±0.02	0.04±0.04	0	0	0	0	0
Epischura lacustris	0	0	0	0	0	0.4±0.1	0.2±0.1	0.1±0.1	0.2±0.1	0.05±0.02
Calanoid copepodites I–V	3.0±0.7	3.0±0.8	3.6±0.6	2.9±0.7	2.7±0.6	3.5±0.3	2.6±0.3	2.6±0.3	2.8±0.4	1.9±0.2
Calanoid nauplii	17.5±2.4	12.4±1.0	8.4±1.3	5.0±0.8	4.3±1.2	4.8±0.6	2.1±0.5	1.6±0.3	1.3±0.3	0.9±0.4
Cyclops vernalis	0	0	0	0	0	0.5±0.2	0.4±0.1	0.6±0.2	0.4±0.1	0.4±0.1
C. bicuspidatus thomasi	6.5±0.7	4.2±0.3	5.2±0.5	4.3±0.7	4.2±0.5	1.1±0.1	0.8±0.1	0.6±0.1	0.7±0.1	0.8±0.1
Tropocyclops prasinus mexicanus	0	0	0	0	0	0.2±0.1	0.06±0.05	0.04±0.04	0.04±0.04	0.05±0.04
Cyclopoid copepodites I–V	10.2±0.6	8.5±0.5	8.9±0.5	8.0±0.4	8.9±0.7	4.1±0.5	3.7±0.4	3.3±0.3	3.6±0.4	3.8±0.4
Cyclopoid nauplii	73.5±5.0	53.8±4.4	56.9±4.5	46.2±4.5	47.1±4.0	8.6±1.8	3.8±0.7	3.4±0.6	3.8±1.0	2.8±0.5
Total Copepoda	116±8.0	83.3±6.4	87.9±6.8	70.0±6.1	70.8±6.6	24.6±1.7	14.9±1.0	13.3±1.0	13.6±0.9	11.6±0.7
Total Crustacea	145±11	95.6±9.6	94.5±7.4	72.3±6.8	73.2±7.1	37.9±1.6	29.0±1.6	28.0±1.2	19.8±1.3	13.5±0.7

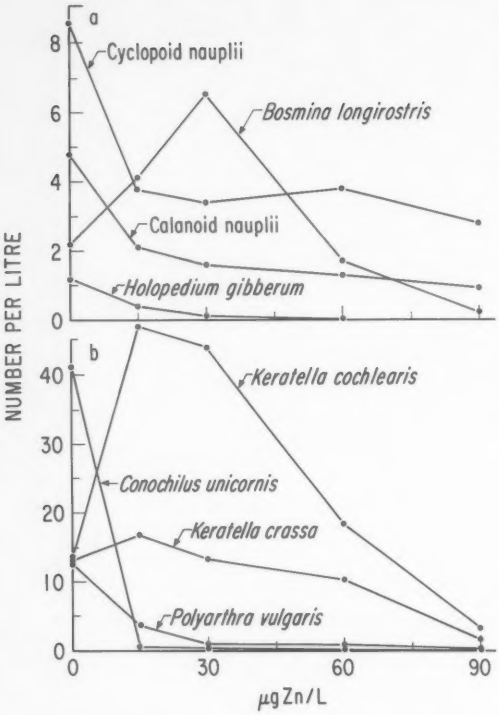

FIG. 2. Average densities of a few stages or species of crustacean zooplankton (a) and planktonic rotifers (b) that exhibited significant increases or decreases (or both) in response to increasing concentrations of zinc in the water in the second dose–response experiment.

indices by every treatment in both experiments (Table 5). The reduction of crustacean zooplankton biomass with increasing zinc concentration was similar to that for net plankton biomass, and crustaceans accounted for about half of the net plankton biomass (Fig. 3).

Bioaccumulation of zinc by each species increased with added zinc but showed few differences among species (Table 6). The average concentration of zinc in *Daphnia galeata mendotae* (adults + young) was significantly lower than in *Holopedium gibberum* ($P < 0.01$) and higher than in calanoid copeods ($P < 0.05$) in control enclosures, as indicated by *t*-tests. Cyclopoid copepods tended to contain more zinc than calanoids, but the difference was not significant.

The effects of cadmium and zinc observed in this and other recent studies provide a basis for comparing the sensitivity and consistency of several indices of stress. Sensitivity is indicated by the amount of change in the percentage value of an index (its value expressed as a percent of mean value for controls) for a given increase in the level of cadmium or zinc. Consistency is indicated by the degree to which an index shows the same relative (rank) sensitivity to similar increases of cadmium or zinc in different ecosystems or at different times in the same ecosystem. Most of the indices used in this study showed somewhat different changes in percentage values in response to a given increase of zinc at different times in Lake Michigan, but their relative (rank) values were similar (Table 7). The differences in percentage values may be due to a progressive increase in the intensity of biological control mechanisms (nutrient limitation, competition, predator–prey interactions) during the course of the summer. Major chemical and physical differences are probably more important in determining the differences in apparent sensitivity among different ecosystems (Table 8). However, the "most reduced species" populations (though the species may vary) are consistently more sensitive than community similarity indices, and species diversity indices and dissolved oxygen consistently rank relatively low. The different indices may also be compared with respect to their detection limits for cadmium or zinc effects. For example, dissolved oxygen was significantly reduced by zinc concentrations as low as 15 μg/L, whereas none of the crustacean species diversity indices (Hill's numbers) was significantly reduced at this level. In Green Bay, Lake Michigan, dissolved oxygen was significantly reduced by a cadmium concentration as low as 0.2 μg/L (Table 8). Reduction of dissolved oxygen indicates a reduction of the photosynthesis/respiration (P/R) ratio and is a useful short-term indicator of metal stress (Giddings and Eddleman 1978; Marshall and Mellinger 1980). All but one of these indices (Table 8) show a lower value for 30 μg/L in Lake Michigan than in ELA Lake 239, indicating a greater apparent sensitivity to zinc in Lake Michigan.

Discussion

Zinc significantly reduced zooplankton populations and several other properties of ecosystem structure and function at concentrations much lower than the lowest levels previously reported to be toxic to zooplankton and well below the concentrations established for protection of freshwater life. The ambient water quality criterion for zinc established by the U.S. Environmental Protection Agency is 47 μg/L as a 24-h average (U.S. EPA 1980). The maximum zinc concentration recommended by the Canadian Inland Waters Directorate for waters with hardnesses in the range of 120–180 ppm $CaCO_3$ is 100 μg/L (Taylor and Demayo 1980). The International Joint Commission recommended a maximum concentration (objective) of 30 μg/L for waters in the Great Lakes (IJC 1977). Significant reductions of chlorophyll *a*, dissolved oxygen, primary productivity, zooplankton populations, and several community level indices for the zooplankton were caused by zinc concentrations as low as 15 μg/L, the lowest concentration tested. Some of the reductions at this concentration were quite severe (>99% in the case of *Conochilus unicornis* populations). Zinc thus appears to be much more toxic to Lake Michigan zooplankton than suspected from the lowest concentrations previously reported to be toxic to zooplankton (Baudouin and Scoppa 1974; Biesinger and Christensen 1972). The difference could be due to the fact that the previous reports were based on studies of selected species in the laboratory and failed to include either the more sensitive species that exist in natural communities or the important

TABLE 4. Average numbers per litre (± SE) of different species of plankton rotifers in control and Cd- or Zn-treated enclosures for two in situ experiments conducted in Lake Michigan during July 10–23 (Experiment 1) and July 6–18 (Experiment 2). Numbers in parentheses indicate number of samples (enclosures). Underlined values are significantly different from controls ($P < 0.05$), as indicated by *t*-tests.

	Experiment 1					Experiment 2				
Species	Controls (6)	3 μg Cd/L (5)	30 μg Zn/L (7)	60 μg Zn/L (6)	90 μg Zn/L (7)	Controls (8)	15 μg Zn/L (8)	30 μg Zn/L (8)	60 μg Zn/L (8)	90 μg Zn/L (8)
Keratella quadrata	9.7±1.6	3.8±1.1	6.7±1.2	9.0±1.8	5.4±0.6	0.1±0.1	0.1±0.1	0.3±0.1	0	0
K. cochlearis	71.8±7.2	27.4±10.1	406±50	214±26	101±6	13.5±1.7	46.9±6.9	44.1±5.1	18.3±2.1	3.3±0.7
K. earlinae[a]	12.7±1.8	3.0±1.1	5.1±1.0	3.5±1.1	1.3±0.5	0	0	0	0	0
K. crassa	0	0	0	0	0	13.3±2.0	16.8±2.9	13.4±2.1	10.3±2.2	1.8±0.4
Kellicottia longispina	38.2±7.9	30.0±10.9	81.4±12.2	60.5±8.8	46.7±4.9	3.2±0.3	4.1±0.7	3.0±0.6	4.1±0.7	1.9±0.4
Ascomorpha ecaudis + A. ovalis	0.8±0.3	0.2±0.2	0	0	0.1±0.1	7.8±1.5	5.4±0.7	3.7±0.7	5.8±0.9	3.5±0.3
Gastropus stylifer	1.5±0.4	0.6±0.4	1.1±0.6	0.7±0.3	0.1±0.1	7.9±1.3	0.7±0.2	0.3±0.1	0.1±0.1	0
Asplanchna priodonta	6.0±2.9	4.6±1.3	0.7±0.4	0	0	1.3±1.2	0.1±0.1	1.3±0.6	0.1±0.1	0
Ploesoma truncatum + P. lenticulare	0	0	0	0	0	3.6±1.5	2.0±0.8	2.3±1.0	1.1±0.4	1.1±0.5
Synchaeta stylata	4.2±0.7	0	0	0	0	0	0	0	0	0
Polyarthra vulgaris	59.0±7.1	57.2±8.4	2.3±0.6	3.8±2.3	1.9±0.7	13.2±3.2	3.6±0.6	0.5±0.2	0.8±0.4	0.1±0.1
P. dolichoptera	14.2±2.1	12.8±4.4	2.6±1.0	0.2±0.2	0.3±0.3	0	0	0	0	0
P. remata	39.0±9.8	32.4±8.8	3.3±0.7	2.8±0.8	1.0±0.7	0.4±0.1	0.4±0.2	0	0	0.1±0.1
P. major	0	0	0	0	0	0.7±0.3	0	0.1±0.1	0.3±0.2	0.1±0.1
Conochilis unicornis	90.5±17.3	6.4±1.5	0.4±0.2	0	0.6±0.6	41.0±4.7	0.5±0.3	0.3±0.2	0.1±0.1	0
Collotheca mutabilis	23.2±3.5	13.5±3.0	20.4±2.6	4.2±0.6	0.3±0.3	9.8±1.9	3.5±0.9	1.0±0.3	0.8±0.4	0
All others	0.3±0.2	0.6±0.4	0.7±0.4	0	0.4±0.2	0.4±0.2	0.9±0.3	0.7±0.2	0.3±0.1	0
Total Rotifera	372±26	190±36	535±56	315±25	159±8	116±11	85.1±10.4	70.7±7.8	41.9±2.0	11.8±1.4

[a]Probably includes *K. c. robusta*.

TABLE 5. Average values (±SE) of two indices of community similarity (*CC* and *PS*), three indices of species diversity (N_0, N_1, and N_2), and one index of evenness for crustacean zooplankton and plankton rotifer communities in control and Cd- or Zn-treated enclosures for two 2-wk in situ experiments conducted in Lake Michigan during July 10–23, 1980 (Experiment 1) and August 6–18, 1980 (Experiment 2). Numbers in parentheses indicate number of samples (enclosures). Underlined values are significantly different from controls ($P < 0.05$), as indicated by *t*-tests.

		Experiment 1					Experiment 2				
Community	Index	Controls (6)	3 µg Cd/L (5)	30 µg Zn/L (7)	60 µg Zn/L (6)	90 µg Zn/L (7)	Controls (8)	15 µg Zn/L (8)	30 µg Zn/L (8)	60 µg Zn/L (8)	90 µg Zn/L (8)
Crustacean	*CC*	92.4±2.2	87.6±2.2	91.2±2.2	82.1±1.3	86.5±2.1	96.6±0.9	93.5±1.3	86.8±2.2	83.7±2.1	79.6±3.4
	PS	90.0±2.0	71.6±2.4	67.3±3.0	57.9±3.2	55.9±3.4	86.8±1.3	81.3±2.1	76.8±2.6	71.5±2.1	57.3±2.6
	N_0	9.5±0.4	8.6±0.4	9.3±0.4	7.7±0.2	8.4±0.4	12.6±0.3	11.9±0.4	10.4±0.4	9.8±0.4	9.0±0.5
	N_1	5.5±0.4	5.7±0.1	6.4±0.2	5.2±0.2	5.0±0.2	8.0±0.3	7.2±0.3	6.2±0.4	6.8±0.2	5.4±0.2
	N_2	4.4±0.4	4.7±0.2	5.3±0.3	4.2±0.3	3.9±0.2	6.2±0.3	5.8±0.2	4.9±0.4	5.8±0.2	4.2±0.2
	N_2:N_1	0.80±0.03	0.82±0.02	0.83±0.02	0.81±0.02	0.78±0.02	0.78±0.01	0.80±0.01	0.78±0.01	0.85±0.01	0.78±0.02
Rotifer	*CC*	95.5±1.9	87.9±1.4	80.1±2.9	69.7±1.3	57.9±5.0	90.2±1.4	78.6±3.0	72.7±2.5	66.8±3.3	52.1±2.2
	PS	90.6±1.3	66.6±2.5	42.6±2.6	39.7±3.0	37.4±3.0	87.5±1.1	42.7±2.0	36.4±2.0	38.1±3.4	33.3±2.2
	N_0	12.8±0.5	11.0±0.3	9.4±0.6	7.5±0.2	5.9±0.7	11.1±0.4	9.1±0.5	8.6±0.5	7.1±0.5	5.1±0.4
	N_1	7.6±0.2	6.5±0.3	2.4±0.1	2.5±0.1	2.5±0.1	6.7±0.5	4.2±0.2	3.5±0.2	4.2±0.3	4.3±0.3
	N_2	6.1±0.2	5.0±0.3	1.8±0.1	1.8±0.1	2.0±0.03	5.1±0.5	2.9±0.2	2.3±0.1	3.2±0.3	3.9±0.3
	N_2:N_1	0.81±0.02	0.77±0.03	0.72±0.01	0.76±0.01	0.82±0.02	0.76±0.03	0.69±0.01	0.67±0.02	0.78±0.01	0.90±0.01

FIG. 3. Net plankton and crustacean zooplankton biomasses (µg dry wt/L) in relation to added zinc concentration in the water in second dose–response experiment. Each point with bars represents mean ± standard error for eight samples. Regression equations ($n = 40$): net plankton biomass = 121 − 0.71 × µg Zn/L ($r^2 = 0.46$); crustacean zooplankton biomass = 67 − 0.54 × µg Zn/L ($r^2 = 0.83$).

species interactions that can compound direct toxic effects (Marshall and Mellinger 1980). The difference in apparent toxicity could also be due to a difference in water chemistry and zinc bioaccumulation. The greater apparent toxicity of zinc to zooplankton in Lake Michigan than in ELA Lake 239 was probably due to the much lower concentration of colloidal organic carbon in Lake Michigan and resulting higher zinc bioavailability and bioaccumulation (Marshall et al. 1981b). Many of the differences in apparent toxicity of zinc in different waters would probably disappear if the toxicity were related to the concentration of zinc in the organisms themselves (bioaccumulation) instead of water quality parameters.

Small differences in zinc bioaccumulation by different species of zooplankton could partially explain some of the observed changes in community structure. The relatively high zinc concentration in *H. gibberum*, for example, could explain its apparent extreme susceptibility to zinc. Makarewicz and Likens (1979) also reported higher concentrations of zinc

TABLE 6. Average concentrations (± SE) of zinc in different categories of crustaceans (μg/g dry wt) from control and Zn-treated enclosures after a 2-wk incubation in Lake Michigan, August 6–18, 1980. Numbers in parentheses indicate number of samples (each consisted of 10–20 individuals except where noted).

Category	Controls	15 μg Zn/L	30 μg Zn/L	60 μg Zn/L
Cladocera				
Daphnia retrocurva	34 (1)	—	—	—
D. galeata mendotae (adults)	31±1 (4)	141±1 (3)	175±10 (3)	380±109 (2)
D. galeata mendotae (young)	29±1 (4)	149±5 (2)	208±12 (2)	—
Bosmina longirostris	27±5 (2)	179±18 (2)	189 (1)	311±38 (2)
Eubosmina coregoni	23±8 (2)	163±28 (2)	205±18 (2)	232±2 (2)
Holopedium gibberum[a]	40±5 (2)	139 (1)	—	700 (1)
Copepoda				
Calanoida (adults)	26±1 (2)	129±24 (2)	162±1 (2)	270±37 (2)
Cyclopoida (adults)	33±3 (2)	175 (1)	214±33 (2)	281±3 (3)
Mixture of crustaceans	29±2 (2)	148±10 (2)	177±14 (2)	432±169 (2)
All samples	30±1 (21)	152±6 (15)	189±7 (14)	347±42 (13)

[a]Two or three individuals per sample.

TABLE 7. Percentages of mean control values for selected indices of zinc stress (30 μg/L) during different periods in this study (Experiments 1 and 2). Underlined values were significantly different ($P < 0.05$) from controls. Numbers in parentheses indicate ranks of percentages shown.

Index	July 10–23, 1980	Aug. 6–18, 1980
Most reduced rotifer population[a]	<1 (1)	<1 (1)
Most reduced crustacean population[b]	18 (2)	5 (2)
Primary productivity	62 (4)	27 (3)
Rotifer community *PS*	47 (3)	42 (4)
Total crustacean density	65 (5)	74 (6)
Rotifer species diversity (N_0)	73 (6)	78 (7)
Total rotifer density	144 (10)	61 (5)
Crustacean community *PS*	74 (7)	88 (9)
Crustacean species diversity (N_0)	98 (9)	82 (8)
Dissolved oxygen (~P/R ratio)	97 (8)	93 (10)

[a]*Conochilus unicornis* during both periods.
[b]*Bosmina longirostris* during first period and *Holopedium gibberum* during second.

in *H. gibberum* than in *Daphnia*, as well as higher concentrations in cyclopoid copepods (*Cyclops* sp.) than in calanoids (*Diaptomus minutus*). Differences in metal bioaccumulation among species could partially account for the fact that metal-contaminated, acidic lakes near Sudbury, Ont., are characterized (in contrast to acidic lakes without metal contamination) by the absence of *H. gibberum* and the dominance of *Bosmina longirostris* (Yan and Strus 1980). Two zooplankton samples collected from our study site with a 243-μm-mesh net on September 29, 1980 were analyzed by X-ray fluorescence spectrometry and were found to contain 22–41 μg Zn/g dry weight (G. T. Tisue, Clemson University, personal communication). These results agree surprisingly well with those calculated from ^{65}Zn analyses of the crustaceans in our controls (Table 6).

The potential long-term effects of cadmium and zinc on the plankton community in Lake Michigan depend on many interacting factors, the most important being the concentration and bioaccumulation of the metals themselves. Muhbaier and Tisue (1981) have argued that the concentration of cadmium in Lake Michigan could increase within a few decades to levels at which deleterious effects on the plankton community are readily observable. A preliminary zinc budget for the southern basin of Lake Michigan indicates that the concentration of zinc in offshore waters may also increase to some extent (G. T. Tisue, Clemson University, personal communication). The pronounced reductions of several structural and functional properties of the plankton community observed for the lowest zinc addition tested in this study (15 μg/L) suggest that significant effects could probably be detected at much lower zinc levels, perhaps only slightly above present concentrations in the lake.

The potential long-term effects of small increases in the aqueous concentrations and bioaccumulation of cadmium and zinc in Lake Michigan would be determined by compensatory reactions (adaptation) at several levels of biological organization. Many of these processes cannot be accounted for in short-term experiments with isolated plankton communities. Exposures as long as 20–40 d may be required for successful adaptation by phytoplankton (Stockner and Antia 1976), and zooplankton probably require longer periods. An increase in the relative abundance of "tolerant" strains or species may be one of the most sensitive indicators of toxic stress (Luoma 1977). Development of tolerance may involve induction of metallothionein synthesis (Brown and Parsons 1978), selection for tolerant clones (Jensen et al. 1974; Murphy and Belastock 1980), or selection for species with low metals bioaccumulation capacities (Briand et al. 1978; Gachter and Geiger 1979). Intrinsic differences in life history patterns (Allen 1976) probably also have different selective advantages. Toxic chemical stress may tend to select for species with higher reproductive rates and smaller body size (Fenchel 1974). Shifts in the size structure of zooplankton communities can affect both predators and prey of the zooplankton (Hall et al. 1976). An increase in the flagellate:diatom ratio can reduce fish production (Greve and Parsons 1977). In acidic, metal-contaminated lakes the dominant zooplankter

TABLE 8. Percentage of mean control values of selected indices of cadmium or zinc stress in different ecosystems. Underlined values were significantly different from controls. Numbers in parentheses indicate ranks of percentages shown.

Index	Green Bay, Lake Michigan[b]		ELA Lake 239[c]		Southern Basin of Lake Michigan[d]		
	0.2 μg Cd/L	2.5 μg Cd/L	3.0 μg Cd/L	30 μg Zn/L	3.0 μg Cd/L	15 μg Zn/L	30 μg Zn/L
Most reduced crustacean population[a]	32 (1)	0 (1)	44 (1)	63 (1)	20 (1)	33 (1)	5 (1)
Total crustacean density	93 (3)	84 (3)	57 (2)	112 (8)	66 (2)	76 (2)	74 (2)
Percentage similarity, *PS*, Crustaceans	81 (2)	76 (2)	97 (8)	93 (4)	79 (3)	94 (5)	88 (6)
Coefficient of community *CC*, Crustaceans	99 (7)	95 (8)	89 (4)	97 (6)	95 (5)	97 (8)	90 (7)
Hill's number N_0, Crustaceans	100 (8)	94 (7)	81 (3)	95 (5)	91 (4)	94 (6)	82 (5)
Hill's number N_1, Crustaceans	95 (6)	85 (4)	94 (6)	84 (3)	104 (7)	90 (3)	78 (3)
Hill's number N_2, Crustaceans	93 (4)	91 (6)	90 (5)	78 (2)	107 (8)	94 (4)	79 (4)
Dissolved oxygen (P/R ratio)	93 (5)	89 (5)	97 (7)	100 (7)	95 (6)	95 (7)	93 (8)

[a]*Eubosmina coregoni*, *Holopedium gibberum* in Green Bay, Lake Michigan; *Diaptomus minutus*, *Epischura lacustris* in ELA Lake 239; *Bosmina longirostris* (Experiment 1) and *Holopedium gibberum* (Experiment 2) in this study in southern basin, Lake Michigan.
[b]Marshall and Mellinger 1980.
[c]Marshall et al. (unpublished data).
[d]This study.

B. longirostris is probably too small to feed on 50% of the phytoplankton, thereby reducing the efficiency of energy transfer from phytoplankton to zooplankton and fish (Yan and Strus 1980). A decrease in the average zooplankter body size would reduce the catch-per-unit effort by planktivorous fish (Hall et al. 1976), and thus would tend to reduce energy transfer efficiency. Alewives (*Alosa pseudoharengus*) up to 150 mm long feed size-selectively on zooplankton in Lake Michigan (Janssen 1976) and form the bulk of the diet of salmonids in the lake (Edsall et al. 1974). Thus, any reduction of average body size or production of zooplankton due to cadmium or zinc stress could reduce alewife production and, indirectly, the stocks of salmon and trout that could be maintained in Lake Michigan.

Acknowledgments

We thank Ron Dana for help aboard the R/V *Ekos*, Karen Stanlaw for technical assistance, and Patricia Tyrolt for typing the original manuscript. Drs Ronald Hall, Marjorie Hall, and Jack Cornett provided helpful suggestions for revision of the manuscript, and the final version was typed by Dr Marjorie Hall. This work was performed under the auspices of the U.S. Environmental Protection Agency.

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Sources of Organic Matter for Reservoir Fish Production: A Trophic-Dynamics Analysis[1]

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ADAMS, S. M., B. L. KIMMEL, AND G. R. PLOSKEY. 1983. Sources of organic matter for reservoir fish production: a trophic-dynamics analysis. Can. J. Fish. Aquat. Sci. 40: 1480–1495.

A trophic-dynamics approach was used to examine the relationships of phytoplankton production, other autochthonous primary producers, and allochthonous organic matter to the organic carbon supply necessary to support the fish community production in 17 southeastern and midwestern U.S. reservoirs. Fish community carbon requirements were estimated using average efficiencies of 10 and 15% per trophic transfer to bracket the range of efficiencies that probably occur in reservoir food webs. At 10% efficiency, most of the reservoir food webs considered appeared to be supplemented significantly by allochthonous organic matter. At 15% efficiency, phytoplankton production accounted for the organic carbon required for fish production in 10 of the 17 reservoirs. In this case, supplementary organic carbon sources were invoked to meet fish production requirements in the remaining seven reservoirs. Our results suggest that, depending on the actual food web efficiencies, autochthonous primary production can often account for the organic carbon supply required for reservoir fish production and that the importance of allochthonous organic matter to reservoir biological productivity may have been previously overemphasized. Although both the morphoedaphic index (MEI) and phytoplankton productivity were strongly correlated with reservoir fish production, a simple relationship does not appear to exist between the MEI and phytoplankton productivity, probably because of the complex aggregate nature of the MEI descriptor.

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Nous avons étudié selon l'approche de la dynamique des niveaux trophiques les relations entre la production phytoplanctonique, les autres producteurs primaires autochtones et la matière organique allochtone, d'une part, et, d'autre part, la quantité de carbone organique nécessaire pour soutenir la production d'une communauté de poisson dans 17 réservoirs du sud-est et du mid-west des É.-U. On a évalué les besoins en carbone de la communauté de poisson à l'aide d'efficacités moyennes variant de 10 à 15 % par transfert trophique afin de délimiter la gamme d'efficacités qui se trouve probablement dans les chaînes alimentaires des réservoirs. Quand l'efficacité s'élevait à 10 %, la plupart des chaînes alimentaires étudiées semblaient recevoir un fort supplément de matière organique allochtone. Dans le cas d'une efficacité à 15 %, la production phytoplanctonique fournissait le carbone organique nécessaire pour la production de poissons dans 10 des 17 réservoirs. Dans les sept autres réservoirs, des sources supplémentaires de carbone organique généraient les besoins pour la production de poissons. Les résultats portent à croire que, selon l'efficacité réelle de la chaîne alimentaire, la production primaire autochtone peut souvent fournir la quantité de carbone organique nécessaire pour la production de poissons en réservoir et qu'on a peut-être trop insisté sur l'importance de la matière organique allochtone pour la productivité biologique des réservoirs. Quoique l'indice morphoédaphique (IME) et la productivité phytoplanctonique étaient

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Printed in Canada (J7202)
Imprimé au Canada (J7202)

en corrélation élevée avec la production de poissons des réservoirs, une simple relation ne semble pas exister entre les deux premiers probablement à cause de la nature globale complexe du descripteur de l'IME.

Received January 17, 1983
Accepted May 30, 1983

Reçu le 17 janvier 1983
Accepté le 30 mai 1983

A number of morphological and chemical parameters have been correlated with fish standing crop and fisheries yield in natural lakes and man-made impoundments (see reviews by Ryder et al. 1974; Ryder 1982). These empirical relationships are of value for fishery management purposes, as they permit predictions of potential fish production from readily available data (Jenkins 1982). Such correlations, however, lack direct causal linkages to production processes (Ryder et al. 1974; Melack 1976; Kerr 1982) and, therefore, provide little insight to the ecological structure and function of the water bodies to which they are applied.

Presumably, the morphoedaphic index (MEI) is indicative of the biological productivity of lakes and reservoirs because morphological and chemical factors, acting through light, temperature, flushing rate, mixing depth, and availability of essential nutrients, are determinants of autochthonous primary production (Kerr and Martin 1970; Henderson et al. 1973; Ryder et al. 1974; Ryder 1982). Because phytoplankton production is usually the primary source of organic matter in most lacustrine systems (Hutchinson 1967; Wetzel 1975), a direct relationship between phytoplankton productivity and fish production is expected, and some success has been reported in relating phytoplankton biomass and productivity to fish yields and standing crop (McConnell et al. 1977; Wolny and Grygierek 1972; Melack 1976; Oglesby 1977; Hecky et al. 1981; Jones and Hoyer 1982). Empirical relationships based on comparisons of observed primary productivity to realized fish production may be more direct and, potentially, more revealing of ecosystem structure and function than the MEI (e.g. Oglesby 1982).

The trophic-dynamics approach has been used to examine the relationship between primary production and fish production in marine pelagic and coastal systems (Ryther 1969; Steele 1974; Mills 1980), estuaries (Peters and Schaaf 1981), and freshwater lakes (Lindeman 1942; Kerr and Martin 1970; Hecky et al. 1981). Comparisons of phytoplankton production to the production of higher trophic levels often suggest the importance of additional organic carbon sources, such as macrophytes (Darnell 1967; Odum and de la Cruz 1967), detritus and/or bacterial production (Hecky et al. 1981), and allochthonous organic matter (Romanenko 1966; Kuznetsov 1968; Sorokin 1972) to aquatic food webs. Correlations of lake and reservoir morphoedaphic features and primary productivity with fish production or yield (Ryder 1965; Jenkins 1967; Melack 1976; Oglesby 1977) harbor the presumption that autochthonous (usually phytoplankton) production is the primary source of organic matter for lacustrine food webs (Ryder 1982; Oglesby 1982), and major allochthonous organic matter inputs should cause significant deviations from expected relationships (Oglesby 1977, 1982).

Reservoirs occupy an intermediate position between rivers and natural lakes in regard to their organic matter sources as well as their morphologic and hydrodynamic characteristics (Ryder et al. 1974; Ryder 1978; Goldman and Kimmel 1978). Despite their widespread distribution and economic importance, reservoirs have received limited ecological and limnological attention compared to that given to natural lakes and streams. Most reservoir research efforts in North America have focused on fisheries management, siltation, or water quality problems and relatively little comparative or holistic investigation has been attempted. Consequently, scientific understanding of reservoirs as ecological systems and, thus, of the mechanisms underlying reservoir fish production is poor (Gerking 1977; Goldman and Kimmel 1978; Benson 1982).

Here we explore the relationship of phytoplankton production and fish production in some U.S. reservoirs for which data on both are available. Our purpose is not to develop or propose an additional empirical index for predicting fish yields but to examine what an analysis of existing data can reveal about reservoirs as ecological systems. We sought to address the following questions: (1) Can phytoplankton production account for reservoir fish production or is it necessary to invoke other sources of organic matter (e.g. allochthonous organic matter, bacterial production, aufwuchs, and macrophyte production) to explain the observed fish biomass in reservoirs? (2) Does reservoir fish community structure reflect the relative importance of allochthonous and autochthonous contributions to the supply of organic matter to a reservoir ecosystem? (3) Is the inferred assumption underlying the MEI as a predictor of fisheries yield (i.e. that fish production is proportional to autochthonous primary production as determined by lake morphometry and water chemistry) supported by the available data? Our primary objectives in considering these questions are (1) to synthesize some of the rather diffuse data and literature relating to the productivity of U.S. reservoirs, and (2) to stimulate further questions, hypotheses, and discussions addressing the ecological structure and function of reservoir ecosystems.

Methods

Sources and Description of Data

Selection of reservoirs included in this analysis was based on the availability of fish standing crop and phytoplankton production data. Reservoir fish standing crop data were provided by the U.S. Fish and Wildlife Service, National Reservoir Research Program, Fayetteville, AR, and phytoplankton productivity estimates were obtained from the literature and unpublished sources. Of 36 reservoirs with multiple-year data on fish standing crops by species and size classes, phytoplankton production measurements were available for only 17, with most of these reservoirs being located in the southeastern or southcentral United States (Table 1). Most reservoirs in the latter category were represented by 2 or more yr of fish biomass data but only 1 yr of phytoplankton production

TABLE 1. Physical and chemical characteristics of the 17 reservoirs included in this analysis.

Reservoir/(state)	Year impounded	Length of growing season (d)	Surface area (h)	Watershed area−surface area ratio	Mean depth (m)	Mean retention time (d)	TDS[a] (mg/L)	MEI[b]
Cherokee (TN)	1942	200	7730	115	12.5	84	130	10.4
Chickamauga (TN)	1940	200	13962	386	5.2	7	100	19.2
DeGray (AR)	1969	215	5431	22	14.9	420	55	3.7
Douglas (TN)	1942	180	7973	148	11.0	55	90	8.2
Hartwell (GA−SC)	1961	210	22663	24	14.0	303	30	2.1
Kentucky (KY−TN)	1944	200	64064	163	5.2	22	85	16.3
Keowee (SC)	1968	195	7511	15	15.2	365	18	1.2
Monroe (IN)	1966	175	4502	25	5.2	208	300	57.7
Moss (TX)	1966	222	455	37	7.3	489	175	24.0
Nickajack (TN)	1967	220	4266	1328	6.9	3	91	13.2
Norris (TN)	1936	200	13841	54	18.3	237	93	5.1
Sam Rayburn (TX)	1965	229	46356	19	4.0	325	100	25.0
Summersville (WV)	1965	150	1102	189	20.7	51	40	1.9
Texoma (OK−TX)	1944	230	36018	286	9.4	288	790	84.0
Tuttle Creek (KS)	1962	175	6394	390	8.2	110	280	34.1
Waco (TX)	1965	238	2942	147	4.6	113	190	41.3
West Point (AL−GA)	1975	218	10467	85	7.0	40	40	5.7

[a]Total dissolved solids.
[b]MEI, the morphoedaphic index, was calculated as total dissolved solids (mg/L)/mean depth (m).

measurements. To the extent possible, we matched the year of primary production measurements to the time of fish collections. In most cases, primary production was measured during the same year or within 1 or 2 yr of fish collections; however, for a few reservoirs, fish and phytoplankton data were obtained several years apart.

Fish standing crop data were usually collected in July or August by the cove rotenone method in two to four coves per reservoir per year. Original fish standing crop data were recorded as weight per unit area by species and size classes within species. We used phytoplankton productivity data obtained with the radiocarbon method (Vollenweider 1971) at monthly, or at least seasonal, intervals.

FISH PRODUCTION ESTIMATES

Fish standing crop data were adjusted to account for incomplete recovery of fishes following rotenone treatment (Grinstead et al. 1977) and for distributional differences of species (and in some cases size classes within species) between open water and cove areas (Hayne et al. 1967). Biomass of each species was categorized as either young-of-the-year (YOY) or fish greater than age 0 (adults) based on the body length of each species at the time of sampling (table 1 in Ploskey and Jenkins 1982). Maximum summer body lengths were derived from published studies on the growth and life history of reservoir fishes, with most of the data obtained from Carlander (1977).

Adjusted standing crops of young-of-the-year and adults of each species were converted to annual fish production by multiplying standing crops by the appropriate annual mean biomass turnover rates (P/B ratios). Data on biomass turnover rates are particularly scarce for individual species and young-of-the-year fish; therefore, we assumed that average turnover rates were 0.7 for adults, 5.0 for shad young-of-the-year (gizzard shad, *Dorosoma cepedianum* and threadfin shad, *Dorosoma petenense*), and 2.0 for other young-of-the-year. Winberg et al. (1972) reported turnover rates of 0.3−0.8 (mean = 0.52) for adult fish depending on their trophic level. Turnover rates of adult percids, northern pike (*Esox lucius*), and cyprinids ranged from 0.4 to 0.7 with a mean of 0.53 (Holcik 1972; Backiel 1971; Kelso and Ward 1972). Most turnover rates reported in the literature, however, are for older (age III^+ and greater) adults experiencing relatively short growing seasons (<150 d) in northern latitudes. Biomass turnover rates of adults in the southern U.S. reservoirs included in this study are probably greater than 0.5 because of the higher water temperatures, longer growing seasons (>150 d), and the younger age of most adults ($<III^+$) than in northern systems. For example, age I^+ to III^+ largemouth bass (*Micropterus salmoides*) in Watts Bar Reservoir, TN, have an annual turnover rate of 0.75 (Adams et al. 1982), and the annual turnover rate of adult largemouth bass in Beaver Lake, AR, is estimated to be 0.8 (A. Houser, U.S. Fish & Wildlife Service, Fayetteville, AR, personal communication). Young fish have more rapid turnover rates than adults; however, rates for both size groups vary according to species, diet, water temperature, and other interacting variables. Turnover rate for juvenile salmon was reported to be 2.0 by Coche (1967) and between 1.75 and 1.95 for several species of small fish in the River Thames (Mathews 1971). Young-of-the-year shad P/B ratios are apparently high in southern reservoirs because of warm temperatures and relatively high food availability. For example, Houser and Netsch (1971) found annual biomass turnover rates of 5−13 for gizzard shad in Beaver Lake, AR.

Estimation of Fish Trophic Level and Organic Carbon Requirements

The trophic level (τ) of each fish species was estimated from food habits data and by assigning a trophic value to each of five food categories. Food habits data, expressed as a percentage of the total volume of food consumed by fish, were reported from a variety of southern reservoirs by Leidy and Jenkins (1977) and summarized in Ploskey and Jenkins (1982). Five food categories (plant, zooplankton, detritus, benthos, and fish prey) were assigned values based on their trophic level in the foodweb. The τ of a species was operationally defined in terms of the trophic levels of its consumed prey. To determine the τ of a species, the weighted τ of its consumed food was added to a value of 1.0 because a predator is one τ higher than its prey. The trophic level (τ) of a fish was therefore calculated as:

$$(1) \qquad \tau_i = 1.0 + \sum_{j=1}^{n} \tau_j (F_{ij}),$$

where $\tau_i = \tau$ of species i,
$\tau_j = \tau$ of prey species j, and
F_{ij} = fraction of the consumed food (volume) of species i consisting of food category j.

This equation is an equivalent, but independently derived, formulation for calculating the trophic level of a consumer (see Carney et al. 1981).

A fish feeding entirely (100%) on living plant material (plant $\tau = 0$) was placed at a τ of 1.0. A pure zooplankton feeder was assigned a τ of 2.0, assuming that zooplankton feed 100% on phytoplankton (τ of zooplankton = 1.0). Fish ingesting 100% detritus were given a trophic value of 1.2, assuming that detritus is of plant origin and that heterotrophic bacteria associated with detritus slightly elevate its trophic value (Bowen 1980) above that of pure plant material (τ of detritus = 0.2). A fish feeding 100% on benthos was assigned a τ of 2.2 (τ of benthos = 1.2), assuming that benthic organisms ingest 75% detritus at level 1.2 and 25% plant material at level 1.0 [1.0 + 1.2 (0.75) + 1.0 (0.25) = 2.2]. Fish prey [bluegill (*Lepomis machrochirus*), shad, etc.] were assigned trophic levels according to their diets, which varied among species. For example, the average diet of a grazer such as adult gizzard shad is composed of 64% detritus, 26% plants, 5% benthos, and 5% zooplankton (Ploskey and Jenkins 1982). The τ of adult gizzard shad is τ = 1.0 + 0.2 (0.64) + 0.0 (0.26) + 1.2 (0.05) + 1.0 (0.05) = 1.24. For a predator such as largemouth bass the calculated τ is 1.0 + 1.2 (0.10 benthos) + 1.85 (0.9 fish prey) = 2.79 (Fig. 1). The 1.85 τ for largemouth bass fish prey was calculated based on the assumption that bass consume a mixture of 50% threadfin and gizzard shad at a combined τ of 1.49, 25% sunfish (*Lepomis* spp.) at 2.1, and 25% freshwater drum (*Aplodinotus grunniens*) at 2.3 [i.e. 1.49 (0.50) + 2.1 (0.25) + 2.3 (0.25)] = 1.85 (Fig. 1).

The annual organic carbon production (mg C · m^{-2} · d^{-1}) required to support the fish community production in each reservoir (summed over all fish species) was then calculated as:

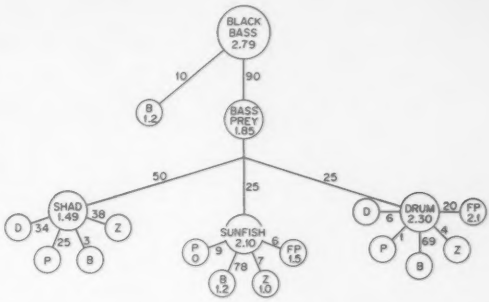

FIG. 1. A three-trophic level food chain illustrating the calculation of trophic levels for a predator (black bass) and its fish prey (shad, *Dorosoma* spp.; sunfish, *Lepomis* spp.; freshwater drum, *Aplodinotus grunniens*). Numbers on lines are the percent of each food item consumed by the next higher trophic level and values inside circles are the calculated trophic levels. D = detritus, P = plant material, B = benthos, Z = zooplankton, FP = larval and juvenile fish prey.

$$(2) \qquad \text{CPR} = \sum_{i=1}^{n} \left(\frac{1}{E}\right)^{\tau_i} (P_i),$$

where

CPR = total organic carbon required by the reservoir fish community,
E = average trophic level conversion efficiency (0 − 1.0) of the foodweb,
τ_i = trophic level of fish species i, and
P_i = annual production of fish species i.

We calculated CPR using average trophic conversion efficiencies of 10 and 15%. For example, at a 10% conversion efficiency, the organic carbon production required to support 1 g of adult gizzard shad production is $(1.0/0.10)^{1.24}$ (1 g) = $10^{1.24}$ = 17.4 g. The 1.24 τ for gizzard shad was derived from equation (1) above (see example). At a 15% conversion efficiency, $(1.0/0.15)^{1.24} = 6.67^{1.24} = 10.5$ g of carbon is required. For largemouth bass at a 10% foodweb efficiency, $10^{2.79}$ = 617 g of organic carbon production is required to support 1 g of bass production.

Fish community structure was compared among reservoirs by calculating the percentages of standing crop and required carbon contributed by each of five trophic groups to the total fish community in each reservoir. Those fish with a calculated trophic level of 1.0−1.99 were assigned to trophic group 1, those falling between 2.0 and 2.24 were assigned to trophic group 2, those from 2.25 to 2.74 to 3, those from 2.75 to 2.99 to 4, and those fish with a trophic level of 3.0 or greater were assigned to trophic group 5.

Assumptions

A number of assumptions regarding both methodological and ecological uncertainties were required for this analysis. We assumed that (1) the net efficiency of each trophic conversion averaged for the entire foodweb is 10−15%

TABLE 2. Sensitivity analysis of assigned fish turnover rates, trophic level values of detritus and benthos, and mean trophic transfer efficiency.

Parameter	Standard value	Sensitivity value	% change from standard	Mean % (SD) change in required carbon[a]
Turnover rate of adults	0.7	0.7±0.2	+30	26.0 (5.0)
Turnover rate of shad young-of-the-year	5.0	5.0±2.0	+40	3.5 (2.3)
Turnover rate of other young-of-the-year	2.0	2.0±1.0	+50	7.1 (5.3)
Trophic level of detritus	1.2	1.5	+25	8.3 (4.1)
Trophic level of detritus and benthos	1.2 and 2.2	1.5 and 2.5	+25 and +14	32.2 (8.8)
Trophic transfer efficiency[b]	10%	8 and 12%	−20 and +20	72.0 (8.0) 35.1 (2.9)

[a]Averaged over all reservoirs and years.
[b] $\frac{\text{Production at trophic level } n}{\text{Production at trophic level } n-1}$.

(Slobodkin 1960; Kozlovsky 1968); (2) food habits for the same sizes and species of fish are similar among reservoirs and years; (3) among species, biomass turnover rates of adults are the same and turnover rates of all young-of-the-year are similar, except shad; (4) biomass turnover rates are similar among species, years, and impoundments; (5) primary productivity and adjusted fish biomass data are representative of entire reservoirs; (6) 1 g wet wt = 1 kcal (1 kcal = 4.186 J) and 10 kcal = 1 g organic carbon; (7) weight-specific carbon content is not significantly different among food categories; and (8) reservoir fish production is controlled primarily by food availability rather than by availability of suitable habitat. Although none of these assumptions are entirely correct, or are without exception, all seem reasonable in terms of the objectives of this exploratory analysis.

Results and Discussion

Sensitivity Analysis and Data Uncertainties

Assumptions relating to turnover rates, trophic levels of food categories, and average trophic conversion efficiencies were examined by sensitivity analysis (Table 2). All parameters were varied from 20 to 50% of their assigned values to assess the effects on estimates of organic carbon required to support reservoir fish production. A 30% change in the biomass turnover rate for adult fish resulted in an average change of 26% in the estimated fish community organic carbon requirement. Variations of 40 and 50% in the values for young-of-the-year turnover rates had a lesser effect (<10%) on required carbon estimates. A 25% increase in the trophic level assignment of detritus also had little effect (8%), but an increase in the trophic level assignment of detritus and benthos together had a relatively large effect (32%) on the required carbon estimates. Assumptions regarding trophic conversion efficiencies have the most significant influence on required carbon estimates, due to the exponential relationship of food chain efficiency to the number of trophic levels. A 20% relative decrease in the efficiency value (from 10 to 8%) increased the carbon required by 72%, whereas a similar increase (from 10 to 12%) resulted in a 35% decrease in required carbon.

Our value for biomass turnover rates of adults (0.70) appears to be realistic, given the available literature values, the species and sizes of fish, and length of growing season for reservoirs included in this analysis. Trophic level assignments for fish consuming detritus (1.2) and benthos (2.2) also seem reasonable, given the present status of knowledge on this subject. The actual trophic level of detritus should not be less than 1.1 or greater than 1.3, assuming that most of the detritus available for ingestion by reservoir organisms is of plant origin. The trophic level of benthic detritivores would not be expected to be greater than 2.3 or 2.4 even if we assumed that benthos were ingesting 100% detritus at trophic level 1.3 or 1.4.

An average value of 10−15% for food chain transfer efficiencies was suggested by Slobodkin (1960) and supported by Mann (1965) and Kozlovsky (1968). Gulland (1070a), Greze (1970), and Steele (1974) demonstrated that a trophic efficiency of 10−15% was exceeded by some consumer trophic levels in marine pelagic foodwebs. However, much lower conversion efficiencies (4−10%) have been reported for phytoplankton−herbivore transfers in productive and unproductive lakes (Wright 1958; Gulati 1975; Makarezicz 1974; Coveney et al. 1977; Lewis 1979). Such low efficiencies are likely explained by incomplete zooplankton harvesting of phytoplankton production (Jassby and Goldman 1974; Kalff and Knoechel 1978; Lewis 1979). Although some of the ungrazed primary production is ultimately consumed through detritus pathways, and trophic conversions may be more efficient at higher trophic levels, such inefficient producer−herbivore transfers must restrict the overall food web efficiency. We estimated fish community carbon require-

TABLE 3. Calculated trophic level and trophic status of young-of-the-year and adult stages for major reservoir fish groups.

Fish groups[a]	Trophic level		Trophic status	
	Young-of-the-year	Adult	Young-of-the-year	Adult
Gizzard shad	1.59	1.24	1	1
Threadfin shad	1.57	1.57	1	1
Carpsucker	1.24	1.24	1	1
Carp	1.60	1.56	1	1
Suckers	2.01	1.97	2	1
Buffalo	2.04	1.83	2	1
Minnows	1.95	1.95	2	1
Redhorse	2.00	2.20	2	2
Bullhead	2.08	2.21	2	2
Madtom	2.06	2.06	2	2
Sunfish	2.11	2.10	2	2
Freshwater drum	2.11	2.30	2	3
Yellow perch[b]	2.04	2.23	2	2
Catfish	2.11	2.99	2	4
Crappie	2.00	2.55	2	3
Temperate bass	2.15	2.79	2	4
Black bass	2.18	2.79	2	4
Walleye[c] and sauger[d]	2.18	2.95	2	4
Flathead catfish[e]	2.18	3.09	2	5
Bowfin	3.00	3.20	5	5
Gar	2.18	3.20	5	5

[a]Some groups contain more than one species.
[b]*Perca flavescens*.
[c]*Stizostedion vitreum vitreum*.
[d]*Stizostedion canadense*.
[e]*Pylodictis olivaris*.

ments, using average efficiencies of 10 and 15% per trophic transfer to bracket the range of efficiencies that probably occur in reservoir food webs.

The fish standing crop and phytoplankton productivity data used in this analysis also introduce uncertainties. Extrapolation of seasonal cove rotenone samples to mean annual standing crop estimates for entire reservoirs is warranted by necessity, but even with correction factors applied, overestimates in fish biomass may occur due to differences in fish distribution between cove and open-water areas (Lambou and Stern 1958; Hayne et al. 1967; Houser and Bryant 1967). The radiocarbon uptake method, introduced by Steeman Nielsen (1951, 1952), is now used routinely to estimate aquatic primary productivity (Goldman 1963; Vollenweider 1971; Lind 1974; Wetzel and Likens 1979). The ^{14}C method is usually assumed to measure net particulate production; however, the accuracy of the method remains uncertain. Comparisons of the radiocarbon method with other measures of planktonic photosynthesis and carbon flow suggest that ^{14}C uptake often underestimates phytoplankton production (Peterson 1980). Therefore, in our estimates of the organic carbon required for fish production (CPR), the most probable errors (overestimated fish production and underestimated phytoplankton production) are in the net direction of phytoplankton production not being able to account for reservoir fish production.

TROPHIC RELATIONSHIPS OF RESERVOIR FISHES

The estimated trophic levels for major fish groups ranged from 1.2 to 3.2, representing a 100-fold difference in the amount of organic carbon required to support a unit of fish biomass (Table 3). Except for bowfin (*Amia calva*) and gar (*Lepisosteus* spp.), which are carnivorous in both young-of-the-year and adult stages (Ploskey and Jenkins 1982), the range in trophic levels was greater for adults (1.2−3.1) than for young-of-the-year (1.2−2.2). Young-of-the-year of most species have similar diets, consisting primarily of zooplankton and benthos, and therefore have a trophic level of about 2.0. Trophic levels of most species groups increased from young-of-the-year to adult as a result of greater use of benthic and fish prey. However, adult gizzard shad and buffalo (*Ictiobus* spp.) decreased from their young-of-the-year trophic levels because detritus and plant material are consumed in larger proportions with increasing body size (Ploskey and Jenkins 1982). Several species and groups of reservoir fishes (threadfin shad, carp, carpsuckers, suckers, minnows, madtoms, bowfins, sunfish, and gars) did not shift appreciably in trophic level between young-of-the-year and adult stages.

CARBON REQUIRED FOR RESERVOIR FISH PRODUCTION

Estimates of organic carbon required to support the observed biomass of each major fish species group are summarized for Keowee and Tuttle Creek reservoirs in Table 4. Data from these two reservoirs serve to illustrate (1) the calculation of total organic carbon production required (CPR) for reservoir fish communities, (2) the extent of year-to-year

TABLE 4. Organic carbon (mg $C \cdot m^{-2} \cdot d^{-1}$) required to support the annual production in each group of the fish community in Keowee and Tuttle Creek reservoirs.

Fish group[a]	Keowee						$\bar{x}$% of total	Tuttle Creek				$\bar{x}$% of total
	1972	1973	1974	1975	1977	1978		1969	1970	1972	1974	
Gizzard shad								142	66	67	67	6
Threadfin shad			15	25	34	33	5					
Carpsucker	1	1	2	1			<1	7	4	23	8	<1
Carp	76	26	48	34	42	30	12	24	49	53	18	3
Suckers			2	2	1		<1					
Buffalo								200	70	236	355	15
Minnows	1	1	2	2	2	7	<1	2	3	4	5	<1
Redhorse	36	14	29	38	43	25	9					
Bullhead	27	21	22	12	17	11	5					
Sunfish	26	57	110	74	54	55	18	7	14	64	100	3
Freshwater drum								97	190	285	541	19
Yellow perch	1	2	7	2	23	19	3					
Catfish			8	9	11	10	2	44	443	176	49	12
Crappie	57	42	116	4	44	4	13	289	39	202	333	15
Temperate bass					2	2	<1	130	37	347	51	10
Black bass	111	155	150	121	81	79	33	105	16	60	123	5
Walleye and sauger								8	18	1	10	<1
Flathead catfish								47	193	124	184	10
Total	336	319	511	324	354	275		1102	1142	1642	1844	

[a]Some groups contain more than one species.

variations in the CPR of individual populations and entire fish communities, and (3) the extremes of reservoir types relative to differences in phytoplankton production rate (PPR) and the total CPR.

The quantities of organic carbon required by reservoir fish communities are relatively constant among years in both Keowee (353 ± 82) and Tuttle Creek (1433 ± 369) (Table 4). However, the carbon required for a particular fish population is considerably more variable. For example, coefficients of variation for CPR by sunfish in Keowee and Tuttle Creek are 55 and 114%, respectively, as compared to 23 and 26%, respectively, for the CPR by the two reservoir fish communities. Annual variations in fish survival and growth due to food and habitat availability, competitive pressures, or spawning and recruitment success are factors that could explain the greater variability in fish population CPR relative to total fish community requirements.

Fish production and phytoplankton production estimates are summarized for all 17 reservoirs included in this analysis in Table 5. Phytoplankton productivity ranged from a low of 67 mg $C \cdot m^{-2} \cdot d^{-1}$ in Tuttle Creek to 1440 mg $C \cdot m^{-2} \cdot d^{-1}$ in Kentucky Reservoir. Only four reservoirs had duplicate years of PPR measurements; however, the values were similar among years. Fish community production varied widely among reservoirs, but, except for Cherokee, annual variations within reservoirs were relatively low (average fish production coefficient of variation = 46%). Insufficient data exist to assess the extent of annual variations in reservoir phytoplankton productivity. However, the coefficients of variation for a 13-yr data set from a productive Russian reservoir (Romanenko 1978) and for 4 yr of data from an oligotrophic Montana reservoir (Woods 1981) were 48 and 23%, respectively. Therefore, the variability associated with annual fish production and primary production in reservoirs appears to be similar.

We approached our first question "Can phytoplankton production account for reservoir fish production or is it necessary to invoke other sources of organic matter inputs to reservoir food webs?" by examining the relationship between reservoir phytoplankton production and fish production (Fig. 2). A linear plot of these two parameters for all 17 reservoirs gave a better fit than a nonlinear relationship and resulted in an r^2 value of 0.34 which is significant at the 0.05 level. By eliminating the three most obvious outliers (Tuttle Creek, Summersville, Keowee), a log−log relationship produced an r^2 of 0.43 ($0.05 > P > 0.01$) which is similar to the coefficients reported by Melack (1976) for African lakes and Oglesby (1977) for a variety of northern lakes. Some justification for omitting these three reservoirs from the regression exists and is discussed in the next section. Most reservoirs with low PPR also had low fish production (Fig. 2). In some cases, however, reservoirs with low or intermediate levels of PPR had disproportionately high levels of fish production (Tuttle Creek, DeGray, Sam Rayburn, Nickajack, Monroe), suggesting that in addition to phytoplankton production other organic matter sources may support the food web in these systems.

The relationship of phytoplankton production to the CPR for reservoir fish communities is presented for average trophic conversion efficiencies of 10 and 15% in Fig. 3. A CPR/PPR ratio of 1.0, represented by the 45° lines in Fig. 3, indicates that PPR can account for the organic carbon required to support the observed fish production. Ratios greater than 1.0 (above the 45° line) imply that carbon fixation by phytoplankton does not provide sufficient organic carbon to support fish production, and ratios less than 1.0 (below the 45°

TABLE 5. Annual fish community production and phytoplankton production (both in mg $C \cdot m^{-2} \cdot d^{-1}$) for the 17 reservoirs included in this analysis. Fish community production was estimated by multiplying adjusted standing crops of young-of-the-year and adults of each species by appropriate biomass turnover rates and summing. Phytoplankton production estimates were obtained by radiocarbon uptake measurements.

Reservoir	Fish production		Phytoplankton production	
	Years	Mean ± SD	Years	Values
Cherokee	1963, 1972–74	38.1±39.0	1969	1416[a]
Chickamauga	1972–73	17.6	1977	1287[b]
DeGray	1975–81	5.5±1.6	1979–80	176, 222[c]
Douglas	1961, 1965, 1973	8.0±6.2	1969	940[a]
Hartwell	1961–63, 1978, 1981	6.0±3.4	1971	800[d]
Kentucky	1963–64, 1974–78	19.0±7.7	1968	1440[e]
Keowee	1972–75, 1977–78	3.0±0.7	1973–74	615, 550[f]
Monroe	1973	13.1	1975–76	343,[g] 412[h]
Moss	1976	12.2	1976	1302[i]
Nickajack	1972	11.1	1973	235[h]
Norris	1960–61, 1969–70, 1975	8.1±5.1	1967	360[a]
Sam Rayburn	1976	10.1	1976	102[j]
Summersville	1968–69, 1971–73	2.5±0.8	1972	466[k]
Texoma	1972, 1976–77, 1980	22.0±9.8	1978	934[l]
Tuttle Creek	1969–70, 1972–74	13.7±3.5	1971	67[m]
Waco	1975	23.0	1968, 1977	857,[n] 770[l]
West Point	1975–81	18.4±11.4	1977	689[o]

[a]Taylor 1971.
[b]Placke and Poppe 1980.
[c]R. H. Kennedy unpublished data.
[d]Abernathy and Bungay 1972.
[e]TVA 1974.
[f]Dillon and Rogers 1980.
[g]Chang and Frey 1977.
[h]Santiago 1978.
[i]Silvey and Stanford 1978.
[j]Lind 1979.
[k]Frazer 1974.
[l]B. L. Kimmel unpublished data.
[m]Marzolf and Osborne 1971.
[n]Kimmel and Lind 1972.
[o]Davies et al. 1980.

line) suggest that PPR exceeds that required for fish community production. We considered overlapping of the 45° line by the 95% confidence limits and shifting the CPR/PPR ratio from above to below the 45° line, to indicate that, statistically, phytoplankton production could account for the estimated fish production, given the variability in the annual fish production data. When the conservative bias of the analysis (i.e. toward overestimated fish production and underestimated PPR) and the additional variability of the PPR data are considered, these criteria are more robust than they initially appear.

Most reservoir CPR/PPR ratios are greater than 1.0 when the food chain transfer efficiency is assumed to be 10% (Fig. 3a). A 15% efficiency assumption lowers the estimated organic carbon requirements of the reservoir fish communities, narrows the confidence intervals, and reduces many of the CPR/PPR ratios to less than 1.0 (Fig. 3b). By the criteria stated above, phytoplankton accounted for fish community carbon requirements in 10 of the 17 reservoirs. However, even at 15% efficiency, the CPR/PPR ratios for Tuttle Creek and DeGray reservoirs remain significantly greater than 1.0, suggesting that organic carbon sources other than autochthonous phytoplankton production are important contributors to the organic matter base of their food webs. Nickajack, Sam Rayburn, Monroe, and Waco reservoirs also have CPR/PPR ratios consistently greater than 1.0, but they are represented by only a single year of fish production data.

Reservoir comparisons — Tuttle Creek Reservoir, in which phytoplankton production is severely light-limited because of high levels of abiogenic turbidity (Marzolf and Osborne 1971), provides an example of a reservoir food web based primarily on allochthonous organic matter. Its apparent net food web efficiency of 20% (Table 6) is anomalously high because of large allochthonous organic matter inputs relative

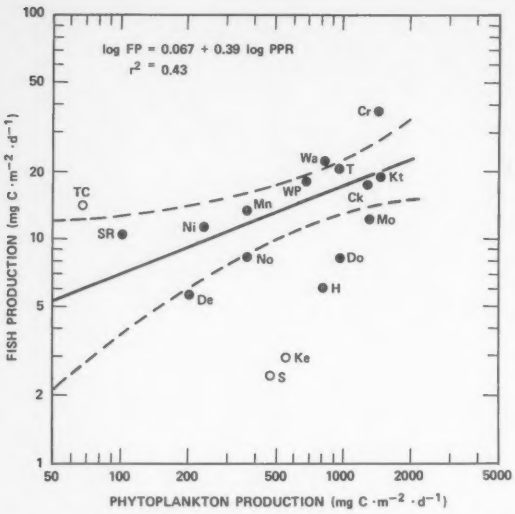

FIG. 2. Relationship between phytoplankton production and fish production for 17 reservoirs located in the southcentral and southeastern United States. The 95% confidence limits of the regression are shown. Reservoirs represented by (○) were not included in the regression (see text).

to low phytoplankton production (Table 5). The hypothesis that allochthonous organic matter forms the base of the Tuttle Creek food web has been supported by laboratory experiments in which *Daphnia* reproduced successfully with only organic compounds adsorbed to silt and clay particles available as an energy source (Marzolf 1981; Marzolf and Arruda 1981).

DeGray and Sam Rayburn reservoirs have two potential organic matter sources in addition to phytoplankton production: (1) allochthonous organic matter and (2) autochthonous production by algae attached to rocks and submerged timber in the euphotic zone. In reservoirs having low phytoplankton productivity, either allochthonous inputs or periphyton production could significantly supplement the base of the food web. Lind (1979) observed abundant epiphytic algal growth on submerged timber in Sam Rayburn Reservoir and hypothesized that the epiphytes provided an important source of organic carbon for consumers. Monroe and Nickajack reservoirs also have identifiable sources of organic matter in addition to phytoplankton production. Profuse growth of rooted macrophytes (*Myriophyllum*) in the shallow upper basin of Monroe Reservoir (Chang and Frey 1977; Landers 1982) likely contributes a significant portion of the organic matter supply to higher consumers in this system. Macrophyte growth in embayments probably also is important to the food web in Nickajack Reservoir (Placke and Poppe 1980). However, fish production in this rapidly flushed, relatively unproductive (235 mg $C \cdot m^{-2} \cdot d^{-1}$) impoundment may also be supplemented by phytoplankton exported from the more productive (1287 mg $C \cdot m^{-2} \cdot d^{-1}$) Chickamauga Reservoir located just upstream.

That only a single year of fish standing crop data is available for Waco Reservoir is particularly unfortunate, because this is the only impoundment in our data set for which an organic matter budget is available. Lind (1971) estimated that allochthonous organic matter provided 23% of the total organic matter supply to Waco Reservoir and concluded that autochthonous phytoplankton production was the major source of organic matter for the reservoir food web. However, the consistent occurrence of the Waco Reservoir CPR/PPR ratio above the 45° line in Fig. 3 indicated that additional organic matter sources are required to support the observed fish biomass. A potential explanation for the disparity between phytoplankton production and fish community carbon requirements in Waco is that the 1975 fish standing crop estimates may have been biased by cove sampling conducted in or near the North Bosque arm (O. T. Lind, Department of Biology, Baylor Univ., Waco, TX, personal communication), which receives 60% of the total allochthonous organic matter loading for the reservoir and is about three times higher in phytoplankton production than other areas of the reservoir (Lind 1971; Kimmel and Lind 1972). Unfortunately, fish standing-crop estimates have not been repeated since 1975 (R. McCabe, Texas Parks and Wildlife Department, Waco, TX, personal communication); therefore, there is no way of judging whether these data are atypical.

Required carbon/PPR ratios that fall significantly below the 45° line in Fig. 3 (Keowee at both 10 and 15% efficiencies, Hartwell and Summersville at 15% efficiency) suggest that (1) the transfer of primary production to upper trophic levels is for some reason inefficient, or (2) fish community production is limited by factors other than food availability. In Keowee and Summersville, shad comprise less than 5% of the fish community standing crop compared to 30% or more in the other reservoirs (except Douglas) (Fig. 4). Without planktivorous clupeids, more energy may flow through detrital food chains rather than through the grazer pathway, and the food chain leading to higher predators may be longer and less efficient (Hecky et al. 1981). However, this reasoning cannot explain the apparent inefficiency of Hartwell where shad are abundant. All three reservoirs are deep (Table 1) and unproductive (Table 5). Their low CPR/PPR ratios could be due to underestimates of fish standing crops in deep reservoirs (Houser and Bryant 1968) rather than to inefficient food web transfers. The CPR/PPR ratio for Norris, another deep, unproductive reservoir, also falls slightly below the 45° line in Fig. 3b.

The fish standing crop in Keowee Reservoir has apparently declined since the start-up of a three-unit nuclear power plant in 1974 (Jenkins 1977). Thermal discharges from the plant, which uses hypolimnetic water for cooling, have increased the reservoir water temperature and depressed the summer thermocline depth from <5 to >20 m (Clugston et al. 1978). Elevated mixed-layer temperatures, which now exceed 30°C in mid- and late summer, may cause physiological stress and reduce fish growth and reproduction by increasing metabolism rates. Additionally, many fishes, such as black basses, that prefer cooler water (Coutant 1975) may avoid the warm coves, and thus cove rotenone sampling in August probably greatly underestimates the fish standing crop in Keowee. Subtle changes in nutrient cycling, turbulence, or mixing could

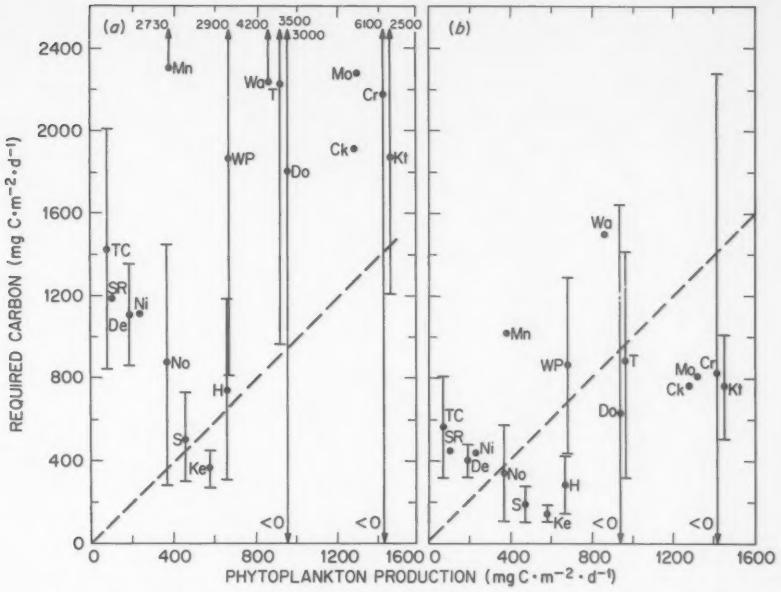

FIG. 3. Relationship between phytoplankton production (PPR) and total carbon required (CPR) by reservoir fish communities (mean ± 95% confidence intervals) at a 10% mean trophic transfer efficiency (a) and a 15% efficiency (b). The diagonal line represents a PPR−CPR ratio of 1.0. Symbols for reservoirs are Cherokee, Cr; Chickamauga, Ck; DeGray, De; Douglas, Do; Hartwell, H; Kentucky, Kt; Keowee, Ke; Monroe, Mn; Moss, Mo; Nickajack, Ni; Norris, No; Sam Rayburn, SR; Summersville, S; Texoma, T; Tuttle Creek, TC; Waco, Wa; West Point, WP.

also affect food web efficiency by influencing phytoplankton species composition or the size distribution of phytoplankton or grazers (e.g. Sheldon et al. 1972, 1977).

Reservoir food web transfer efficiencies — Net food web transfer efficiencies (Table 6), which represent the apparent percentage of phytoplankton production converted to fish production in each reservoir (assuming no other organic matter sources and complete conversion of phytoplankton production to fish production), are independent of trophic transfer efficiency assumptions. Apparent food web efficiencies ranged from 0.53 to 4.7% with a mean of 1.98% (excluding Tuttle Creek and Sam Rayburn) and generally paralleled the required carbon−PPR ratios (Fig. 3). Our values for reservoirs are considerably higher than those previously reported for most marine and freshwater systems (Table 6). Several reservoirs included in this analysis, including those having relatively high CPR/PPR ratios (Fig. 3) and carbon transfer efficiencies (Table 6), were sampled within 10 yr of their impoundment. Terrestrial detritus derived from inundated soils and vegetation enhances fish production in reservoirs for 5−10 yr after filling (e.g. Ploskey 1981) and, therefore, probably contributes to high apparent food web efficiencies in the newer impoundments. Autochthonous primary producers other than phytoplankton and labile allochthonous organic materials also supplement reservoir food webs to some extent and, undoubtedly, are partially responsible for these high values. The higher system efficiencies for these reservoirs may be due primarily to the fact that our estimates are based on the production of the entire fish community, rather than on the yield or production of only commercially harvested species which usually comprise only 30−50% of the total standing crop (Gulland 1970b; Henderson et al. 1973). Given the unquantified relationship between fish yield and production, the variability of the fish production data, and the unknown variability of the primary production data, most of our carbon transfer efficiency estimates for southern reservoirs may not differ significantly from those previously estimated for other freshwater systems.

FISH COMMUNITY STRUCTURE

Our second question "Does fish community structure reflect the relative importance of autochthonous and allochthonous organic carbon contributions to reservoir food webs?" was addressed by comparing reservoirs for which multiple years of data were available for fish community standing crop. Surprisingly, no consistent differences in either standing crop or required carbon patterns were apparent even among limnologically dissimilar reservoirs (Fig. 4). Lower trophic groups accounted for most fish community standing crop in most reservoirs, whereas upper trophic

TABLE 6. Net food web transfer efficiencies (fish production/phytoplankton production) expressed as percentages for reservoirs in this study and other aquatic systems.

		Other aquatic systems			
Reservoir	Fish production/ phytoplankton production (±SD)	System	Fish production or yield/primary production	Reference	Comments
		6 Asian reservoirs	0.07	Sreenivasan 1972	Fish yield
Cherokee	2.69±2.76	4 European lakes and reservoirs	0.11	Oglesby 1977	Fish yield
Chickamauga	1.37	2 Scotland lakes	0.06	Oglesby 1977	Fish yield
DeGray	2.75±0.80	Lake Tanganyika	0.45	Hecky et al. 1981	Fish yield
Douglas	0.85±0.66	English Channel	0.58	Harvey 1950	Fish production
Hartwell	0.75±0.43	Block Island Sound	0.60	Merriman and Warfel 1948	Fish production
		Nova Scotia coast	0.38		
Kentucky	1.32±0.53	Mid-Atlantic bight	0.20	Mills 1980	Fish production
Keowee	0.79±0.18	Gulf of Maine	0.38		
Monroe	3.47	North Sea	0.80	Gulland 1970a	Fish production
Moss	0.94	Peruvian upwelling	0.60		
Nickajack	4.70	Temperate seagrass system	1.37	Adams 1976	Fish production
Norris	2.25±1.42				
Sam Rayburn	9.90				
Summersville	0.53±0.36				
Texoma	2.34±1.05				
Tuttle Creek	20.45±5.19				
Waco	2.68				
West Point	2.67±1.66				
Mean (without Tuttle Creek and Sam Rayburn) = 1.98					
Mean (all reservoirs) = 3.07					

groups were more important in regard to organic carbon required for fish production (Fig. 4). Trophic group 1 (filter-feeding planktivores and benthic detritivores) accounts for over 50% of the standing crop in most reservoirs but only 16% of the required carbon. Trophic groups 3, 4, and 5 (sight-feeding predators and piscivores) contribute only 26% of the biomass but 64% of the required carbon. This result is not surprising from an ecosystem energetics viewpoint; however, it should be noted that strategies for the management or regulation of reservoir biota could differ, depending on whether standing crop, production, or energy requirements of the fish community are considered. In terms of system energetics, most reservoirs could probably support more fish at the lower trophic levels, such as shad, but not increased biomass of top-level predators. This suggests that management practices aimed at enhancing the production of appropriate-sized, low trophic level, forage fish may provide the best approach for enhancing sport fish (predator) production, as opposed to accelerated stocking of game fish, which places greater energy demands on the reservoir food web. However, such an energetics-based management strategy does not consider competitive interactions which may occur between forage and game fishes at early life history stages.

Fish standing crop patterns in Summersville and DeGray reservoirs differed somewhat from other systems, with trophic groups 2 (sunfish) and 4 (black bass) more dominant in Summersville and biomass distributed more evenly among trophic groups 1–4 in DeGray. Similarly, in terms of required carbon, trophic groups 2 and 4 appear to be slightly more important in the less-productive reservoirs (Summersville, DeGray, and Keowee), with Tuttle Creek being a notable exception. Both Summersville and DeGray have small benthic components but dominant predator components in their fish communities (Fig. 4). Although the two impoundments differ greatly in basin morphology, flushing rates, and other characteristics (Table 1), their fish communities may be influenced by similarities in the organic matter base of their food webs. We suspect that periphyton production (growth of attached algae on steep rock walls in Summersville and on rocks and submerged timber in DeGray and Sam Rayburn) may contribute significantly to the food web in these reservoirs. Macroinvertebrate densities on submerged timber were 11 times greater in Lewis and Clarke Lake and four times greager in Lake Francis than on adjacent bottom sediments. In both of these lakes, macroinvertebrate densities were significantly correlated with periphyton biomass (Claflin 1968; Cowell and Hudson 1967). Attached algal growth could be more important to reservoir game fish production than reflected by its contribution to total system primary production because it supports a localized concentration of organisms (i.e. an aufwuchs community) which may be more efficiently exploited by larger consumers than is the highly

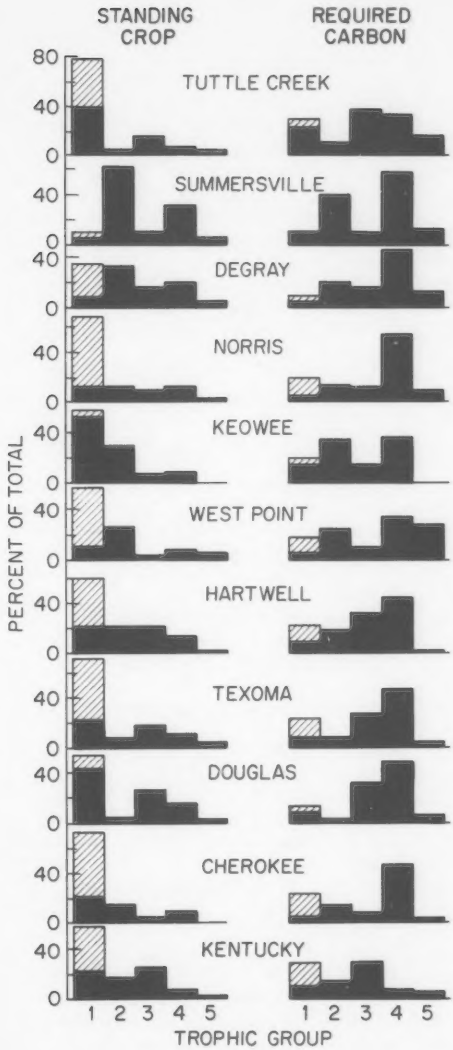

FIG. 4. Percent of reservoir fish community standing crop and organic carbon required to support the fish community production in five trophic groups. Trophic groups were assigned according to calculated trophic level (see text). For trophic group 1.0, cross-hatched portions are planktonic grazers and solid portions are benthic detritivores.

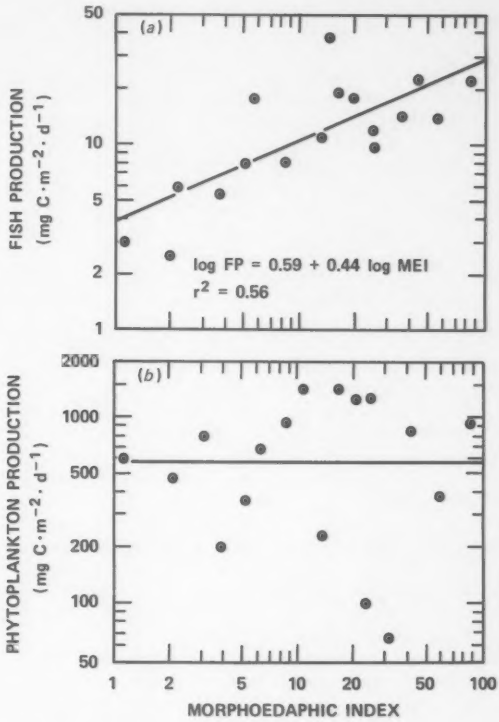

FIG. 5. Relationship between the morphoedaphic index (MEI), fish production, and phytoplankton production for the reservoirs included in this analysis. The slope of the regression line for MEI and phytoplankton production is not significantly different from zero ($P > 0.90$).

dispersed plankton community.

The apparent lack of distinguishable patterns in fish community structure among reservoirs that differ considerably in phytoplankton productivity and in the relative importance of autochthonous and allochthonous organic matter inputs may be due to the highly interconnected nature of grazer and detritus pathways and the pivotal role of benthic detritivores in reservoir food webs (Goldman and Kimmel 1978). Whether derived primarily from autochthonous or allochthonous sources of organic matter, a significant fraction of the biologically available organic matter in most reservoirs enters the benthic detritus subsystem via sedimentation of organic particles and contributes to the production of benthic-feeding fishes. For example, a relatively large benthic detritivore component occurs in the fish communities of reservoirs with very low primary production but high allochthonous inputs (Tuttle Creek) and those with high autochthonous production (Kentucky, Cherokee, Douglas, Texoma) (Fig. 4, Table 5). However, Summersville Reservoir, which because of its canyon-like basin has a reduced benthic area relative to its pelagic volume, essentially lacks a benthic component in its fish community (Fig. 4). Such interactions among organic matter sources, trophic pathways, and basin morphology may underlie the conservative nature of fish production systems described by Kerr and Martin (1970) and Kerr (1982).

Phytoplankton Production, Fish Production, and the MEI

The MEI is a robust predictor of fisheries production and yield in a variety of freshwater systems including reservoirs (Ryder et al. 1974; Ryder 1982; Jenkins 1982); however, its ecological basis remains unclear. Presumably, the MEI is broadly indicative of both nutrient availability in a system as reflected by the total dissolved solids concentration, and the capacity of the system to process energy and materials, as reflected by the mean depth (Oglesby 1977, 1982). Additionally, availability of light and nutrients controls autochthonous primary production, thereby providing the organic matter base of the food web and thus determining the magnitude of fish production (Ryder et al. 1974; Ryder 1982). We examined the relationships between the MEI, phytoplankton production, and fish production to test the validity of these presumed linkages.

A significant correlation exists between the MEI and fish community production for the 17 reservoirs included in this analysis (Fig. 5), as has been previously reported for larger data sets (e.g. reviews by Ryder et al. 1974; Jenkins 1982). Additionally, phytoplankton productivity and fish production were significantly correlated (Fig. 2), as previously reported for natural lakes, ponds, and some reservoirs (Melack 1976; Oglesby 1977; Liang et al. 1981), thus supporting the presumed food chain linkage between autochthonous primary production and reservoir fish production. However, the MEI was not correlated with phytoplankton production (Fig. 5, $r^2 < 0.05$, $P > 0.9$) and, therefore, the inferred assumption underlying the MEI as a predictor of fisheries yield (i.e. that fish production is proportional to autochthonous primary production as determined by lake basin morphology and water chemistry) is not supported by these data. Henderson et al. (1973) and Brylinsky and Mann (1973) also reported similarly inconclusive relationships between the MEI and phytoplankton production.

That a simple, direct relationship does not appear to exist between the MEI and phytoplankton productivity should not be particularly surprising. Mean depth may not relate well to phytoplankton production because the depth of the euphotic zone delimits the region where photosynthesis occurs. Certainly, in the absence of light limitation, phytoplankton productivity is related to nutrient availability, as witnessed by an extensive literature on phytoplankton ecology and lake eutrophication. Although simple in form, the MEI reflects a complex aggregation of covarying internal factors, processes, and feedback mechanisms (Ryder 1982; Oglesby 1982; Kerr 1982) which apparently integrate in such a way as to influence fish production more significantly, or perhaps just more consistently, than phytoplankton production.

Summary and Conclusions

We believe that our trophic-dynamics approach for evaluating the importance of allochthonous and autochthonous sources of organic matter to aquatic food webs is applicable to most lentic ecosystems. Although it is commonly assumed that allochthonous inputs significantly supplement the organic matter base of reservoir food webs (Romanenko 1966; Sorokin 1972; Straskrabova 1975), the actual extent of allochthonous organic matter incorporation into food webs and its subsequent contribution to fish production is unknown. If the proportion of refractory material is considerably greater in fluvial inputs of organic matter than in autochthonous primary production, as is generally believed (e.g. Wetzel 1975), much of the allochthonous organic matter entering reservoirs may not enter the food web (Odum and Prentki 1978; Goldman and Kimmel 1978; Kimmel 1983).

Trophic-dynamics analyses are particularly sensitive to assumptions of trophic conversion efficiency (Table 2), and, unfortunately, the most appropriate efficiency for various aquatic ecosystems continues to be debated. If the average net trophic conversion efficiency is 10% or less, then our data suggest that most of the reservoir food webs considered here are supplemented to a considerable extent by allochthonous organic matter (Fig. 3a). However, if this efficiency is 15% or higher then autochthonous phytoplankton production can account for the organic matter necessary to support total fish community production in 10 of the 17 reservoirs (Fig. 3b). In this case supplementary organic carbon sources must be invoked to meet the requirements of fish production in the remaining seven reservoirs (Monroe, DeGray, Nickajack, Tuttle Creek, West Point, Waco, and Sam Rayburn). Autochthonous production by macrophytes and/or attached algae appears likely to supplement phytoplankton production in Monroe and DeGray reservoirs. We hypothesize that phytoplankton production in Nickajack Reservoir is limited by its rapid flushing rate (mean annual retention time = 3 d), but is supplemented both by macrophyte production and by phytoplankton imported from a larger, more-productive impoundment (Chickamauga) upstream. Terrigenous organic detritus derived from the flooded soils and vegetation of recently filled reservoir basins may also contribute to the high CPR/PPR ratios of DeGray, Monroe, West Point, Waco, Nickajack, and Sam Rayburn reservoirs. Only in Tuttle Creek, where autochthonous primary production is severely limited by abiogenic turbidity, does allochthonous organic matter clearly make a substantial contribution to the reservoir food web and ultimately to fish community production.

Numerous assumptions involving both methodological and ecological uncertainties were required for this analysis. Our conclusions, therefore, must be considered preliminary, but hopefully they will stimulate more ecosystem-oriented questions and research on reservoirs. Within the limitations of the available data and our knowledge of reservoir ecological processes, our analysis suggests that:

1) Depending on the actual efficiency of reservoir food webs, autochthonous primary production can often account for the organic carbon required for reservoir fish community production, and the generally presumed importance of allochthonous organic matter to reservoir food webs may have been overemphasized;
2) A basic similarity in fish community trophic structure among relatively dissimilar reservoirs may be due to the highly interconnected nature of grazer and detritus pathways and the pivotal role of benthic detritivores in reservoir food webs; and
3) Although both the MEI and phytoplankton productivity can be related to fish production, a simple relationship

does not appear to exist between the MEI and phytoplankton productivity, probably because of the complex, aggregate nature of the MEI descriptor.

Better information on the autochthonous and allochthonous organic matter inputs to reservoirs, on the biological availability of these inputs, and on the actual trophic transfer efficiencies of aquatic food webs is required to distinguish the relative contributions of various organic matter sources to reservoir fish production. Clearly, detailed investigations of the production and food web processes underlying reservoir productivity are required to advance our understanding of reservoirs as ecological systems and, thereby, enhance our abilities to predict, manage, and improve the fisheries potential of multiple-use impoundments.

Acknowledgments

This manuscript has benefited from the helpful suggestions of S. M. Bartell, A. P. Covich, J. W. Elwood, L. J. Paulson, and W. Van Winkle. Special thanks go to R. A. Ryder and D. A. Schlesinger for their many constructive comments. This research was sponsored by the Office of Health and Environmental Research, U.S. Department of Energy, under contract W-7405-eng-26 with Union Carbide Corporation.

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Analysis of Catch/Effort Data: A Comparison of Three Methods

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ROFF, D. A. 1983. Analysis of catch/effort data: a comparison of three methods. Can. J. Fish. Aquat. Sci. 40: 1496 – 1506.

The models of Schnute and Deriso are compared with a simple autoregressive model (SA model). Comparisons are made using both stepwise and omnibus prediction. In the latter case predictions are made for at least 3 or 10 yr ahead. The SA model is shown to be consistently better at predicting both catch and catch-per-unit effort than either of the other two models. Furthermore, the percentage error is frequently sufficiently small to make the predictions useful for stock assessment. It is shown that in practice the Schnute and the Deriso models are variants of the SA model. It is suggested that catch and effort data cannot be used to establish equilibrium catches. The reasons for this are that unique equilibria probably do not exist and the catch/effort data are generally too unreliable to detect anything except major fluctuations in population size. It is suggested that catch-and-effort data can be used by adopting strategies designed to track the population fluctuations.

ROFF, D. A. 1983. Analysis of catch/effort data: a comparison of three methods. Can. J. Fish. Aquat. Sci. 40: 1496 – 1506.

Les modèles de Schnute et de Deriso ont été comparés avec un simple modèle autorégressif (modèle SA). Des prédictions à la fois en gradins et omnibus ont été utilisées dans ces comparaisons. Dans le cas des prédictions omnibus, leur portée est d'au moins 3 à 10 ans à l'avance. Le modèle SA donne constamment de meilleures prédictions, tant des prises que des prises par unité d'effort, que l'un ou l'autre des deux autres modèles. En outre, le pourcentage d'erreur est souvent assez faible pour que ces prédictions soient utiles dans les évaluations de stocks. Nous démontrons qu'en pratique, les modèles de Schnute et de Deriso sont des variantes du modèle SA. Nous sommes d'avis que les prises en état d'équilibre ne peuvent être déterminées sur la base des données sur les prises et l'effort. C'est que des équilibres uniques n'existent probablement pas et que les données de prises/effort sont généralement trop peu fiables et ne permettent de détecter que des fluctuations majeures de taille d'une population. Nous suggérons que, pour pouvoir utiliser les données sur les prises et l'effort, il faut adopter des stratégies conçues de façon à suivre les fluctuations de population.

Received April 22, 1980
Accepted June 6, 1983

Reçu le 22 avril 1980
Accepté le 6 juin 1983

THERE are probably no fish stocks for which a thorough and quantitatively adequate analysis of population dynamics is available. For most stocks our knowledge is so fragmentary that all the available mathematical models make very sweeping assumptions. One of the most renowned models in this regard is that of Schaefer (1954). The model uses only catch-and-effort data and seeks to establish the relationship between catch and effort at equilibrium. The assumptions within this model and its modifications due to Pella and Tomlinson (1969) and Fox (1970) are without doubt oversimplifications (Silliman 1971).

Walter (1973, 1978) attempted to make these models more realistic by introducing a time delay in the population response to density and a recruitment function. But these models, like the others, predict only the equilibrium yield and do not predict the trajectory a stock will follow in the immediate future. Yet it is precisely this information that is required in the current assessment of stocks and the setting of quotas.

Printed in Canada (J6044)
Imprimé au Canada (J6044)

Walter (1976) examined this problem theoretically assuming the Schaefer model to be an appropriate description of the fishery. A major problem in the use of this model is that the ratio of the population biomass at the beginning and the end of the year is required, and this ratio is unlikely to be obtainable in practice. The simplest method of overcoming this difficulty is to replace the differential equation with a difference equation. Walters and Hilborn (1976) and Uhler (1978) used the Schaefer model in this form whereas Schnute (1977) took a slightly different approach to derive a discrete form of the Schaefer model. Both of these discrete formulations take the form, $C_{t+1} = f(E_{t+1}, E_t, C_t)$, where C_t and E_t are the catch and effort at time t. For a stock that consists of several age groups a more valid model might be $C_{t+1} = g(E_{t+1}, E_t, E_{t-1}, \ldots\ldots, C_t, C_{t-1}, \ldots\ldots)$. Deriso (1980) developed a model of this type. His model predicts the catch-per-unit effort in year t from the 4-yr catch-and-effort data and the data from year $t-k$, where k is the earliest age of significant vulnerability. The Schnute model contains four parameters and the Deriso model seven parameters. Thus both models

require a reasonably long sequence of catch/effort data to be fitted.

In this paper I address the question 'do the Schnute or Deriso models predict future catches or catch-per-unit effort better than a simpler model?' This simpler model is derived by the following argument. Most demersal species of fish comprise many age groups and thus neither recruitment nor fishing can substantially change population size over a short time period. The catch-per-unit effort in year t is therefore about equal to the catch-per-unit effort in year $t-1$. The catch in year t (C_t) is thus about proportional to $E_t C_{t-1}/E_{t-1}$ where E_t is the fishing effort in year t. To construct a predictive model of catch we regress C_t on $E_t C_{t-1}/E_{t-1}$ to give the autoregressive model:

$$C_t = A + B\, E_t\, C_{t-1}/E_{t-1}$$

where A and B are the regression coefficients. I shall refer to this model as the SA model (Simple Autoregressive model). To obtain the predicted catch-per-unit effort I have simply divided the predicted catch by the effort. The SA model, being developed from simple biological considerations, falls between the heuristic time series approach adopted by Mendelssohn (1980) or Saila et al. (1980) and the mechanistic models of Schnute (1977) and Deriso (1980). However, the SA model is strictly a predictive model and its utility is to be judged on its ability to predict catches or catch-per-unit effort rather than any underlying biological rationale. Generally, in this paper, the term model refers to the equations relating catch or catch-per-unit effort at time t with the relevant quantities at time $t-1$. Prediction is not limited to 1 yr ahead as the catch at time $t+m$ can be predicted from the predicted catches at times $t, t+1, \ldots\ldots t+m-1$. Strictly speaking, tests of the three models are tests of the estimation procedures. It may always be argued that the model is correct but the parameters cannot be estimated. However, the methods used here to estimate the parameter values in the three models are statistically sound and probably the best available. Hence, comparisons of the three estimation procedures can be regarded as comparisons of the three models.

There are two approaches to testing the utility of a model. First, we might construct hypothetical populations that may or may not satisfy the assumptions of the model. The catches predicted from such simulated populations can be compared with those predicted from the model. The second method is to examine the ability of a model to predict the observations from a real stock (Deriso 1980; Stocker and Hilborn 1981). In this paper I have adopted this second approach. The Schnute and Deriso models predict both the time series of future catches and the sustainable catches. In the present analysis I shall consider primarily the short-term prediction of catches. I shall, however, consider what characteristics of the models are responsible for the quality of the predictions and hence whether long-term predictions are likely to be reliable.

Comparison of the Schnute and SA Models

I compared the performance of the Schnute and SA models on 21 stocks of demersal fish species covering a wide range of species and geographic areas (Table 1). One stock, 3LNO American plaice, *Hippoglossoides platessoides*, is a composite and was used because assessments have been done on both the separate and grouped data. There is evidence that the stocks are separate (Pitt 1973).

Both models were fitted by minimizing the mean square error. In the case of the Schnute model the procedure outlined in the section 'Summary for the User' of Schnute (1977) was adopted. The linear and nonlinear methods both with and without the "error parameter," σ, were tried: all gave qualitatively the same results and only the results of the nonlinear version incorporating σ will be presented. One unforeseen feature of the procedure suggested by Schnute is that although estimates of the parameters might be obtained, it is possible for the model to be unable to make a prediction as a result of the occurrence of the logarithm of a negative number. This problem was encountered several times. The SA model was fitted using the standard linear regression method.

A logical choice for the statistic with which to compare the two models is the mean square error (MSE). The method that consistently gave a lower MSE would be considered the better method. Although a model might be better than other models, it might still be unacceptable because its predictions differ too widely from the observed values to be of practical use. It is not immediately clear from the MSE when the deviations between predicted and observed catches are unacceptably high. For example, suppose in one case the predicted and observed values are 15 and 10, respectively, and in another case they are 105 and 100. In both instances the MSE is 25 but the latter case the prediction is clearly 'better' than the former because the percentage error is small. To compare the % error we compute:

$$\frac{|\text{Observation} - \text{Prediction}|}{\text{Observation}} \times 100\%.$$

In the first case this gives 50% and in the second 5%, which more clearly indicates the practical significance of the two estimates. To provide an index of the % error in the methods I define the following quantity:

$$\text{MA\%E} = \frac{1}{(T_2 - T_1 + 1)} \sum_{t=T_1}^{T_2} \frac{|O_t - P_t|}{O_t} \times 100\%$$

where MA%E stands for Mean Absolute Percentage Error. T_1, T_2 are, respectively, the initial and final years in the series and O_t, P_t are the observed and predicted catches in year t. The index indicates whether a prediction is of practical value. For assessment purposes an error of 30% is tolerable (A. T. Pinhorn, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld., A1C 5X1, personal communication). Because the MA%E is an average we require a MA%E that is substantially less than 30% unless the variance in the statistic is very small. As a rough measure of acceptability I have adopted a level of 20%. If one method is better than another in all instances but gives a MA%E in excess of 20%, it is still of little practical value.

There are basically two ways to compare the performance of a model. First, we can fit the model to the data utilizing the complete data set and then compare prediction and observation over the entire history. In the present case this entails

TABLE 1. A list of stocks used to compare the performance of the Schnute and SA models.

Stock	Number of years of data	Source
Cod		
3M[b]	18	Unpublished[a]
3NO	24	"
3PS	20	"
2J, 3KL	17	"
Barents Sea	21	Garrod 1969
Bear Island	21	"
Iceland	21	"
Faroe	21	"
Yellowtail flounder		
Southern New England	24	Lux 1969
Georges Bank	24	Lux 1969
Cape Cod	19	Lux 1964
American Plaice		
3L	23	Unpublished
3N	23	"
3O	23	"
3LNO	23	"
3PS	23	"
Redfish		
3M	22	Unpublished
3LN	21	"
St. Lawrence	25	"
Haddock		
Georges Bank	51	Deriso personal communication
Halibut		
Pacific Area 2	47	Ricker 1975

[a]All unpublished data from Fisheries and Oceans, St. John's, Nfld.
[b]Stocks designated by alphanumeric characters refer to stocks from the indicated statistical areas around Newfoundland.

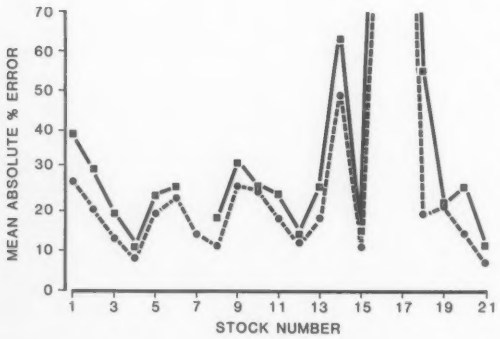

FIG. 1. MA%E of the Schnute (■) and SA (●) models from stepwise prediction: 1, 3M cod; 2, 3NO cod; 3, 3PS cod; 4, 2J, 3KL cod; 5, Barents Sea cod; 6, Bear Island cod; 7, Icelandic cod; 8, Faroe cod; 9, Southern New England yellowtail; 10, Georges Bank yellowtail; 11, Cape Cod yellowtail; 12, 3L American plaice; 13, 3N American plaice; 14, 3O American plaice; 15, 3LNO American plaice; 16, 3PS American plaice; 17, 3M redfish; 18, 3LN redfish; 19, St. Lawrence redfish; 20, Georges Bank haddock; 21, Pacific area 2 halibut.

predicting the catch in year t from the observations in year $t-1$. I shall refer to this type of prediction as stepwise prediction. The second approach is to divide the data set into two groups, not necessarily of equal size, and fit the model to the data of the first group. The model is then run forwards to predict the catches observed in the second data set. In this instance, the catch in year t is predicted from the predicted catch in year $t-1$. I shall refer to this type of prediction as omnibus prediction. This second type of comparison is more realistic.

The results obtained for stepwise prediction are shown in Fig. 1 for the MA%E and Table 1 for the MSE. To standardize the data the maximum catch and effort in each stock was set to 1 by dividing through by these maxima. The following points are evident from Table 1 and Fig. 1:

1) In 19 stocks the MSE and MA%E of the SA model is less than that obtained with the Schnute model. In the Icelandic cod stock the SA model fits but although the parameters of the Schnute model can be estimated, prediction is not possible in at least 1 yr because of the occurrence of the logarithm of a negative number. In the remaining case (3M Redfish) the fit of both models is too poor to be of any practical use (MA%E = 145% for the Schnute model and 149% for the SA model).

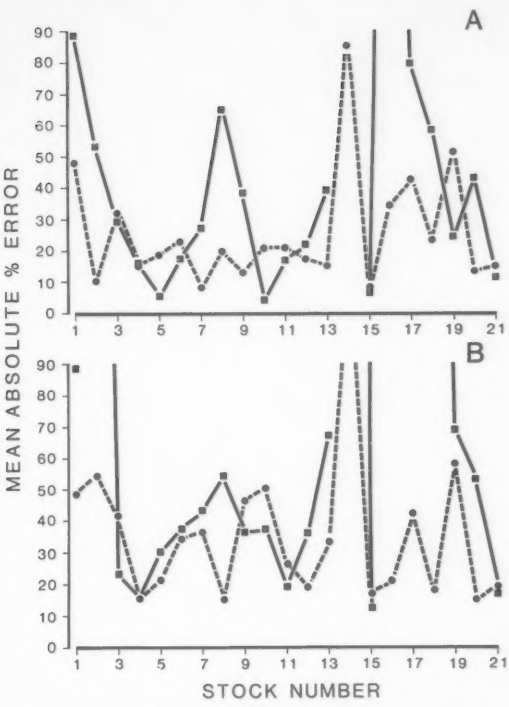

FIG. 2. MA%E of the Schnute (■) and SA (●) models from omnibus prediction starting in year 16. (A) Maximum projection time of 3 yr; (B) maximum projection time of 10 yr. Stock Nos. as in Fig. 1.

TABLE 2. A comparison of the relative performance of the Schnute and SA models: the MSE computed from stepwise prediction of 21 fish stocks.

Stock	I[a]	r^2[b]	MSE	
			Schnute	SA
Cod				
3M	0.85	0.51	0.1063	0.0252
3NO	0.92	0.84	0.0144	0.0061
3PS	0.96	0.74	0.0230	0.0095
2J, 3KL	0.73	0.85	0.0066	0.0041
Barents Sea	0.88	0.64	0.0188	0.0142
Bear Island	0.61	0.59	0.0238	0.0151
Iceland	0.75	0.00	NC[c]	0.0149
Faroe	0.92	0.37	0.0299	0.0112
Yellowtail flounder				
Southern New England	0.92	0.84	0.0290	0.0152
Georges Bank	0.89	0.87	0.0191	0.0094
Cape Cod	0.78	0.43	0.0359	0.0167
American Plaice				
3L	0.98	0.92	0.0057	0.0034
3N	1.00	0.91	0.0184	0.0053
3O	0.98	0.89	0.0181	0.0054
3LNO	0.86	0.95	0.0053	0.0027
3PS	0.99	0.37	0.1830	0.0499
Redfish				
3M	0.99	0.26	0.1860	0.0560
3LN	0.90	0.53	0.4196	0.0131
St. Lawrence	0.91	0.93	0.0126	0.0050
Haddock				
Georges Bank	0.91	0.81	0.0202	0.0057
Halibut				
Pacific Area 2	0.71	0.91	0.0055	0.0020

[a]Schnute's Failure Index.
[b]Coefficient of determination.
[c]Not calculated.

2) For both models there is a highly significant correlation between the MSE and MA%E (using Spearmans rank correlation; for the Schnute method $r_s = 0.676$, $t = 3.89$, $n = 20$, $P < 0.001$ and for the SA model $r_s = 0.651$, $t = 3.74$, $n = 21$, $P < 0.01$).

3) The MSE and MA%E of the two methods vary in concert (see Table 1 for MSE and Fig. 1 for MA%E).

4) Schnute (1977) suggests a failure index, I, as a measure of goodness of fit. The failure index I can vary between 0 and 1 with a high value indicating a poor fit. In all cases I is large (Table 1). However, it is uncorrelated with both the MSE ($r_s = 0.173$, $t = 0.74$; $n = 20$; $P > 0.25$) and the MA%E ($r_s = 0.425$, $t = 1.99$, $n = 20$, $P > 0.05$).

5) A similar index for the SA model is the coefficient of determination r^2. Like I, r^2 can vary between 0 and 1 but in this case a high value indicates a good fit. However, even a low value of r^2 may be associated with small errors of prediction. For example, in the Icelandic cod stock $r^2 = 0$ but the MA%E is only 14%. As is to be expected the MSE and r^2 are highly correlated ($r_s = 0.651$, $t = 3.74$, $n = 21$, $P < 0.01$). The MA%E and r^2 are not correlated ($r_s = 0.297$, $t = 1.35$, $n = 21$, $P > 0.05$).

6) The MA%E obtained with the SA model is less than 20% in 12 stocks. For the Schnute model the MA%E is less than 20% in 6 stocks.

In the second method of comparison (omnibus prediction), I used the first 15 yr of the time series of catch-and-effort data to fit the particular model. I then projected the model ahead a maximum of 3 yr and 10 yr (the time series was not always long enough to project ahead these maximum lengths). The results using the MSE and MA%E are qualitatively the same and only the latter are presented (Fig. 2). As with the stepwise prediction the Schnute model 'failed' in a particular stock (3O American plaice) because of the occurrence of the logarithm of a negative number. In 15 of the remaining 20 stocks the SA model gave smaller values of MA%E. The same result is obtained using the MSE. This number is greater than expected by chance ($\chi^2 = 5$, df $= 1$, $P < 0.05$) indicating that the two models differ significantly in their relative performance. In the 3-yr projection the SA model produced predictions with a MA%E of less than 20% in 11 cases. When the maximum prediction span was extended to 10 yr this number dropped to 7 cases. The respective numbers for the Schnute model are 5 and 4 cases. Thus the SA model is useful for prediction in twice as many cases as the Schnute model.

TABLE 3. Parameter estimates for the Schnute model. Stocks in which the inequality $0 < r - qE < 1$ holds for all years are marked with a +. Stocks in which $-1 < r - qE < 0$ holds for all years are marked with a −.

Stock	r	q	k	σ
Cod				
3M	−0.37	−0.38	−8.68	0.14
3NO	−0.01	0.20	0.53	0.14⁻
3PS	0.25	0.25	12.1	0.13⁺
2J, 3KL	0.39	0.38	6.46	0.07⁺
Barents Sea	0.22	0.22	6.41	0.15⁺
Bear Island	0.32	0.27	5.25	0.16⁺
Iceland	−1.49	−1.26	−2.64	0.32⁻
Faroe	0.32	0.25	8.59	0.14⁺
Yellowtail flounder				
Southern New England	0.04	0.37	−0.57	0.17
Georges Bank	0.20	0.25	5.47	0.18
Cape Cod	−0.26	−0.43	−1527	0.12
American Plaice				
3L	0.01	0.06	8.37	0.07
3N	−0.05	−0.02	430.3	0.15⁻
3O	0.13	0.26	−31.07	0.30
3LNO	0.25	0.22	7.24	0.10⁺
3PS	0.00	0.09	351.5	0.56
Redfish				
3M	0.13	0.21	8.53	0.44
3LN	−0.49	−0.52	−5.30	0.20
St. Lawrence	0.12	0.23	8.00	0.16
Haddock				
Georges Bank	0.12	0.34	9.48	0.17
Halibut				
Pacific Area 2	0.43	0.40	4.77	0.09⁺

Relationship Between the Schnute and SA Models

It is evident from Fig. 1 and 2 that the Schnute model and the SA model tend to vary together. When one model fits well the other is also likely to fit relatively well. In this section I demonstrate that the two models are in practice closely related. The parameter estimates for the Schnute model are given in Table 3. These estimates are based on the complete time series for each stock. To demonstrate the relationship between the Schnute and SA models we first note the following two approximations:

$$e^a \sim 1 + a \qquad |a| < 0.7$$

$$\ln(1 + a) \sim a \qquad |a| < 0.7$$

As described earlier, before analysis, the catch-and-effort data for each stock were divided by the largest catch and effort from that stock: thus for each stock $0 < C_t < 1$, $0 < E_t < 1$ over the observed values and the above approximations generally hold for the transformed C_t and E_t. For convenience let us express the Schnute model as:

$$\bar{C}_t = \frac{qk}{r} E_t \ln\left[1 + \frac{A}{B} \cdot \frac{e^B - 1}{1 - e^{-A}} \quad (1 - e^{-D})\, e^{\sigma}\right]$$

where:

$$A = r - q\,E_{t-1}$$

$$B = r - q\,E_t$$

$$D = \frac{r\,C_{t-1}}{qk\,E_{t-1}}.$$

Because $0 < E < 1$, then if $r > q$ and $r < 1$ then $|r - qE| < 1$. Stocks for which this inequality holds are indicated in Table 3. Hence A and B are both sufficiently small for the approximation to be valid and we have:

$$\bar{C}_t \sim \frac{qk}{r} E_t \ln\left[1 + \frac{A}{B}\frac{B}{A}(1 - e^{-D})\, e^{\sigma}\right]$$

$$\frac{qk}{r} E_t \ln\left[1 + e^{\sigma} - e^{-D+\sigma}\right]$$

Now $r \sim q$ and k is generally large relative to r and q (Table 3). The parameter σ is very small and hence we can make use of the second approximation to give:

$$\bar{C}_t \sim e^{\sigma} \frac{E_t C_{t-1}}{E_{t-1}}.$$

The principal difference between the above approximation to the Schnute model and the SA model is that in the approximation $\bar{C}_t$ is constrained to pass through the origin. Although this is clearly a logical necessity in a model based on 'mechanistic' reasoning, it is not a necessity for a heuristically derived predictive model. Forcing the equation to go through the origin may substantially reduce the fit between C_t and $E_t C_{t-1}/E_{t-1}$ and hence the predictive power of the model. If this reasoning is correct there should exist a positive correlation between the absolute value of the intercept of the SA model and the MSE of the Schnute model, i.e. as the intercept moves away from 0 the Schnute model should show an increasingly poor fit (increasing MSE). All intercept values of the SA model are positive. There is a highly significant correlation between the intercept of the SA model and MSE from the Schnute model ($r_s = 0.57$, $t = 2.91$, $n = 20$, $P < 0.01$). Furthermore in the stock in which the Schnute model 'failed' (Icelandic cod) the intercept is over twice as large as in any other stock. This stock was excluded from the correlation analysis as no MSE can be calculated, although it would be reasonable to assign it the highest rank with respect to MSE. This would increase the significance of the correlation.

An example of a poor fit of the Schnute model and a good fit are shown in Fig. 3. In both fish stocks there is a highly significant regression between C_t and $E_t C_{t-1}/E_{t-1}$ (for 3LN

FIG. 3. Predicted (●) catches from the Schnute model and observed (+) catches (C_t) versus $E_t C_{t-1}/E_{t-1}$. Solid line, approximate Schnute formula: broken line, regression line (SA model). (A) 3LN redfish, (B) 3L American plaice.

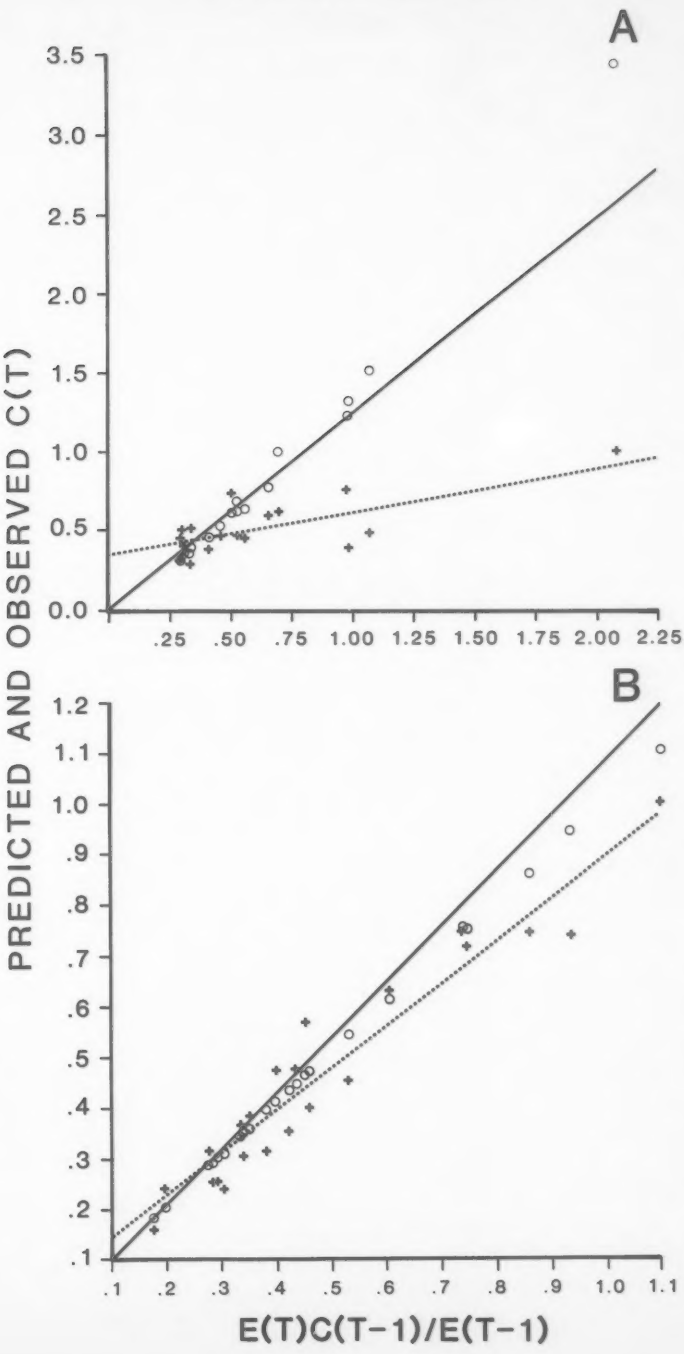
A
B
PREDICTED AND OBSERVED C(T)
E(T)C(T−1)/E(T−1)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
.25 .50 .75 1.00 1.25 1.50 1.75 2.00 2.25
1.2
1.1
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
.1 .2 .3 .4 .5 .6 .7 .8 .9 1.0 1.1

TABLE 4. Two comparisons of the Deriso, Schnute, and SA models in predicting catch-per-unit effort in two fish stocks.

Stock	MSE			MA%E		
	Deriso	Schnute	SA	Deriso	Schnute	SA
Stepwise prediction						
Haddock	0.0968	0.2553	0.0851	15	27	14
Halibut	0.0094	0.0129	0.0059	9	11	7
Omnibus prediction						
Haddock	0.3761	15.2	0.1777	26	337	18
Halibut	0.1994	0.1460	0.0151	66	55	11

redfish $r = 0.73$, $t = 4.54$, $n = 20$, $P < 0.001$ and for 3L American plaice $r = 0.96$, $t = 15.63$, $n = 21$, $P < 0.001$). But for 3LN redfish the intercept of the regression (which is of course the SA model) is relatively large (0.3436 compared to 0.0496 for 3L American plaice). The Schnute model predicts very poorly for medium to large values of $E_t C_{t-1}/E_{t-1}$ although the SA model clearly does reasonably well. The approximate formula for the Schnute model predicts the values from the Schnute model in both stocks very well. The predictions from the Schnute model fit the 3L American plaice data much better than the redfish data but still not as well as the SA model (MSEs of 0.0057 and 0.0034, respectively).

Comparison of the Deriso, Schnute, and SA Models

The Deriso model predicts catch-per-unit effort whereas the Schnute and SA models predict catch. A simple method to estimate catch-per-unit effort with these last two models is to divide the predicted catch by the effort. I have adopted this procedure, recognizing that to a degree it is statistically 'unfair' as these estimators were not derived to predict catch-per-unit effort. Nevertheless, if one of these proves 'better' than the Deriso model, then, the statistical problems notwithstanding, we can still state that it is a better predictor than the Deriso model.

For the purpose of comparison I selected the two stocks previously analyzed by Deriso (1980), the Georges Bank haddock and the Pacific area halibut. For all comparisons I used the parameter estimates derived by Deriso using the full data sets. For 'fair' comparison I therefore estimated the parameters for the Schnute and SA models also using the full data sets.

The MSE and MA%E from the stepwise predictions are shown in Table 4. In both stocks the ranking, from best to worst predictor, is SA, Deriso, Schnute. The difference between the SA and the Deriso models is small. Also shown in Table 4 are the results of an omnibus prediction across the complete time series. In this case the SA model is substantially better than either of the other two models.

To compare the performance of the models at omnibus prediction across 3- and 10-yr intervals I divided the time series into 3- or 10-yr blocks and initiated predictions in the 1st year of each block. The results derived from an analysis

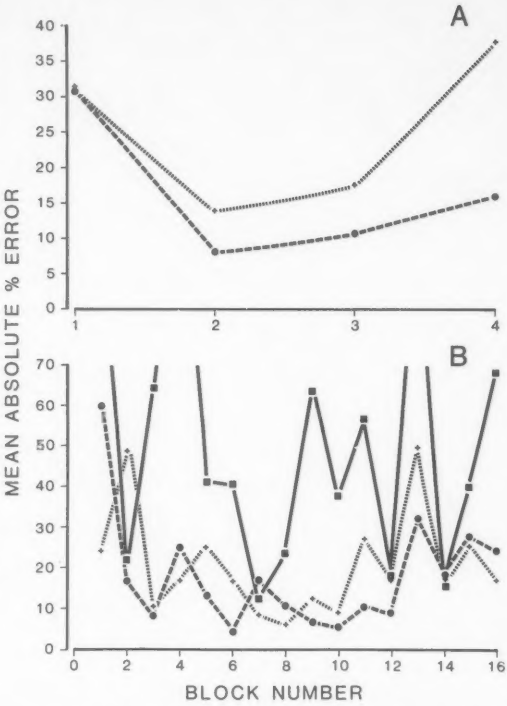

FIG. 4. MA%E from the omnibus predictions of the Deriso, Schnute, and SA models. Data from the Georges Bank haddock. The MA%Es of the Schnute model exceeded 100% in all cases for the 10-yr predictions and are not shown. (A) 10-yr blocks, (B) 3-yr blocks. (--+--) Deriso, (--■--) Schnute, (--●--) SA.

of the MSE or MA%E are qualitatively the same and only the MA%E results are shown in Fig. 4 and 5. Considering first the haddock stock: the Schnute model is clearly the worst predictor. The MA%E in all 10-yr blocks exceeded 100% and are not shown in Fig. 4. The Deriso and SA models are comparable when compared with 3-yr blocks, the MA%E of SA model exceeding that of the Deriso model in 7 of the 16 blocks. However, the SA model has a smaller MA%E in all four blocks of the 10-yr predictions.

In the case of the halibut data, the Deriso model is the worst predictor and the SA model is again the best. The SA model has a smaller MA%E than the Schnute model in 10 of the 14 3-yr blocks and in all 4 of the 10-yr blocks.

Relationship Between the Deriso and SA Models

In both the haddock and halibut stocks the effort has remained relatively stable over the years (see fig. 3 of Deriso 1980). Thus we may substitute the mean effort in the Deriso model to obtain the following approximate equations. For halibut:

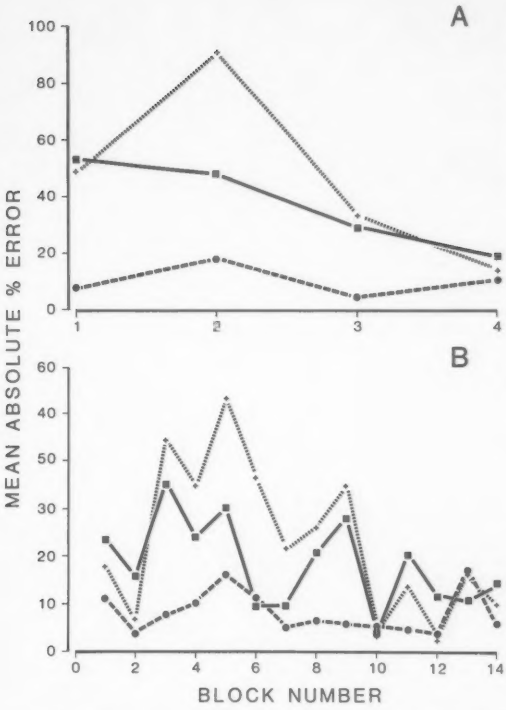

FIG. 5. MA%E from the omnibus predictions of the Deriso, Schnute, and SA models. Data from the Pacific area 2 halibut. (A) 10-yr blocks, (B) 3-yr blocks. (--+--) Deriso, (--■--) Schnute, (--●--) SA.

$$c_{t+1} \sim 1.05c_t - 0.26c_{t-1} + 0.00c_{t-2} - 0.00c_{t-3} + \frac{1.63c_{t+1-k}}{(0.88c_{t+1-k}+1)}.$$

For haddock:

$$c_{t+1} \sim 1.10c_t - 0.44c_{t-1} + 0.08c_{t-2} - 0.00c_{t-3} + \frac{1.35c_{t+1-k}}{(0.20c_{t+1-k}+1)}$$

where c_t is the catch-per-unit effort in year t. In both cases considerable weight is given to the catch-per-unit effort of the previous year as in the SA model. The coefficients of catch-per-unit efforts of $t-2$ and $t-3$ are negligible. For the halibut stock c_t has varied from 3.5 to 4.5: the range in the final term of the approximate formula is 1.38 to 1.67. In the haddock stock c_t has varied from 4.7 to 43.8 but this causes a variation in the final term of the approximate formula of only 2.84 to 3.78.

The heavy dependence of prediction on the immediately preceding year is clearly seen in the figures of Deriso's paper. The predicted catch-per-unit effort appears to be out of phase with the observed catch-per-unit effort by 1 yr. This is demonstrated in Fig. 6 in which I have redrawn Fig. 4 from Deriso (1980). In the lower part of the figure I have shifted the predicted catch-per-unit effort curve back 1 yr. There is clearly a good match between the two lower traces, indicating that the Deriso model in this case is little more than the approximation $c_{t+1} \simeq c_t$. For many demersal fish species this approximation is reasonable as the large number of age classes buffers the population against major short-term fluctuations in size.

Do the Deriso or SA models do better at predicting catch-per-unit effort in haddock and halibut than the approximation $c_{t+1} = c_t$? To compare these three models I computed the coefficient of determination between predicted and observed catch-per-unit effort and the MSEs. The results are given in Table 5. For the halibut all three models are more or less equal. In the case of the haddock, the Deriso model and the SA model do somewhat better than the approximation $c_{t+1} = c_t$.

Discussion

A model or method, no matter how realistic or reasonable it might appear on theoretical grounds, should attain general currency only when it has been proven to be appropriate in the real world. The surplus production model is highly suspect on theoretical grounds and suffers from the disadvantage (or advantage) that it is almost impossible to test because it predicts only where a stock will end up after a number of years of consistent fishing mortality. The methods outlined in this paper depend only upon catch-and-effort data: this is both their strength and weakness. It is their strength because such data are relatively easy and cheap to gather. It is their weakness because they may not be capable of encompassing the complexity that may be inherent in biological systems.

Both with respect to predicting future catches and catch per unit, the SA model performs better than either the Schnute or Deriso models. In some stocks there may be statistical problems such as trends or systematic errors in the residuals of the models. However, the consistently better performance of the SA model indicates that it is in general the best model. Some of the parameters of the Deriso model can, in principle, be estimated from biological data. This might improve the predictions. However, the parameters used in the two stocks examined in this paper are taken directly from Deriso (1980) and are considered to "compare favorably with published parameter values" (Deriso 1980). In their analysis Stocker and Hilborn (1981) concluded that the Schnute method should "be tried for any specific stock." The results of the present analysis suggest that this is an optimistic assessment: it not only performs consistently worse than the SA model but can also be wildly inaccurate in some cases. To measure the relative performance of a method, Stocker and Hilborn (1980) suggested a statistic based on the mean squared error (MSE). Whereas such a measure can be used to compare several models, the MA%E has the advantage that the utility of an estimator is immediately clear. I concur with their view that a variety of methods should be tried, including methods based on time-series analysis. The validity of the SA model is to be measured first and foremost on pragmatic grounds; provided it produces adequate predictions it can be used. Its use should

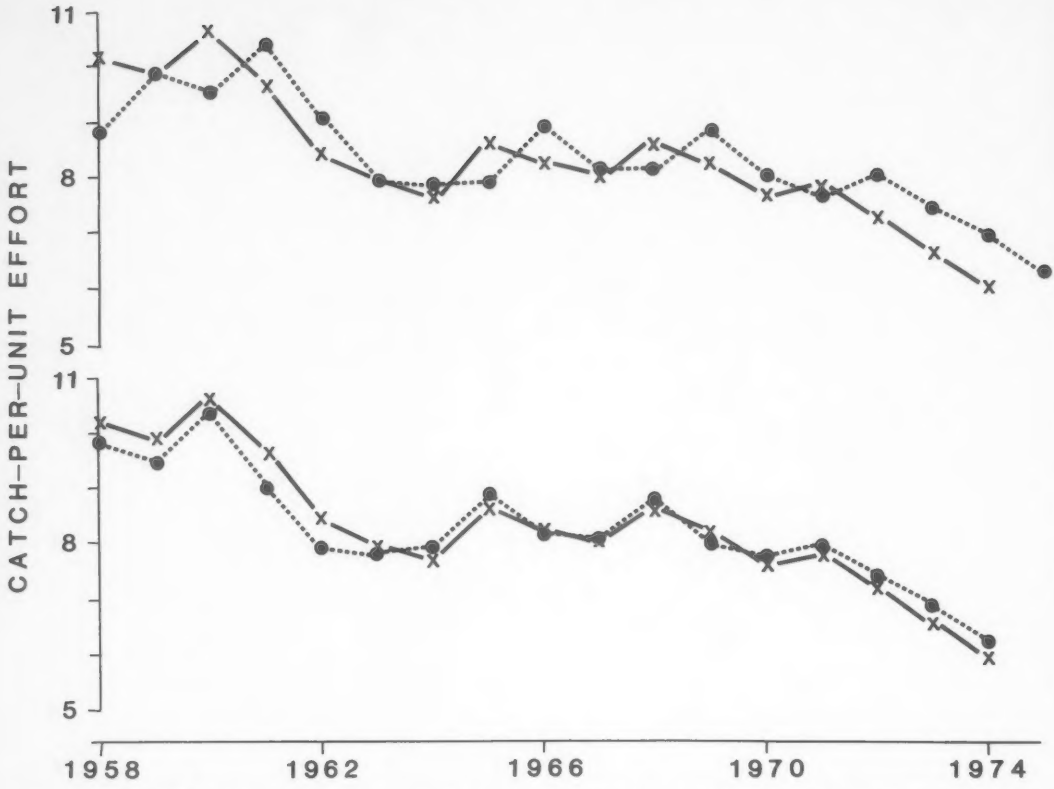

FIG. 6. Predicted (●) and observed (x) catch-per-unit effort for Pacific halibut of Areas 1 and 2. Prediction from the Deriso model. In the lower pair of traces the predicted catch-per-unit effort has been shifted back 1 yr. Upper traces redrawn from Deriso (1980).

TABLE 5. Two comparisons of the performance of three models that predict catch per unit effort, c_{t+1}.

	r^2			MSE		
Stock	$c_{t+1} = c_t$	Deriso	SA	$c_{t+1} = c_t$	Deriso	SA
Halibut	0.86	0.87	0.93	0.005	0.0094	0.0059
Haddock	0.76	0.87	0.88	0.1728	0.0968	0.0851

be preceded by an examination of its ability to predict future catches by dividing the time series into two segments, one for preliminary fitting and the other for testing. If it produces acceptable predictions the full data set can be used to estimate the parameters for future predictions. In their analysis Stocker and Hilborn (1980) restricted their attention to predictions only 1 yr ahead. The present analysis suggests that predictions can be made, in some cases, for at least 10 yr ahead.

The SA model is not proposed as a model that predicts equilibrium yields. The Schnute and Deriso models do predict equilibrium yields. The poor performance of the Schnute model in predicting future catches and its development on a weak theoretical base (the logistic equation) suggest that predictions of optimum catch and effort are probably unreliable. The Deriso model is based on a much more realistic theoretical foundation. However, the large number of parameters to be estimated make it usable only on data sets comprising many years or for which there are biological data that can be used to estimate some parameters. In such cases it is likely that the data exist to generate more realistic simulation models. Of the three stocks examined by Deriso (1980), two have been analyzed via simulation modeling: Sissenwine (1977) produced a simulation model of the yellowtail flounder (*Limander ferruginea*) and Southwood (1968) a simulation model of Pacific halibut (*Hippoglossoides stenolepis*). The population dynamics of Pacific halibut has also been studied with cohort analysis (Hoag and McNaughton 1978). In both stocks the additional biological information that can be incorporated into a simulation model makes this approach preferable to a model based solely on catch-and-effort data. This does not necessarily imply, however, that the predictions will be more accurate. But, in general, the incorporation of addi-

tional information should increase precision: the results of the two approaches could, of course, be compared. The Georges Bank haddock stock has also been studied via cohort analysis (Hennemuth et al. 1980) and hence a model incorporating more biological realism than the Deriso model might be constructed. The importance of cohort analysis is that it can establish the historical changes in population size and hence provide data on stock–recruit relationships and/or baseline data for the fitting or verification of a simulation model. It is pertinent to ask 'in how many stocks is cohort analysis impractical'? Of those species examined in this paper, only the redfish, *Sebastes* sp., are difficult to age and make cohort analysis unreliable at present. The principal problem with other species is that either the catch at age data are not available or that the time series is too short for cohort analysis. The former is a historical problem that cannot be solved and hence in these instances models based on catch-and-effort data may be necessary. The lack of historical catch at age data is not a problem for most stocks of the Newfoundland region as an admirable series of aged samples has been maintained for many years (personal observation, for a listing of available documents see index and listing of titles of ICNAF meeting documents available from V. M. Hodder, ICNAF, P.O. Box 638, Dartmouth, N.S., Canada). If the time series of catch data is too short for cohort analysis, then it will also be too short to apply even the simplest catch/effort model. Although the SA model could in principle be fitted to 5 yr of data, the confidence limits about any projection would be so large as to make the prediction meaningless.

Ideally one would like a model that could be used to project ahead ad infinitum. However, this may not be generally possible and a far shorter time horizon must be adopted. This calls for management strategies that are adapted to the uncertainties of the future and of our predictions. Given that catches are predictable for at least the next 3 yr, how might this information be used to decide quotas? Firstly, we should note that for groundfish stocks, where there are relatively large numbers of age classes, catch-per-unit effort (C_t/E_t) may be a reasonable measure of the health of the stock [this is certainly not true for pelagic stocks (Butterworth 1979)]. Thus a consistent downward trend in C_t/E_t can be taken as an indicator of a stock decline. Initially such a decline might not be too serious as it may simply be the result of the removal of the older age classes and not an indicator of a potential stock collapse. However, if the trend is found in a well-established fishery and, given the present effort the SA model predicts a continued decline in catches and hence C_t/E_t, then caution is advised. With only catch/effort data we are playing a game of blindman's buff over the catch/effort phase plane. We presume that over this surface there exists a set of equilibrium states; this, however, is only an assumption and, given the interrelationships between populations, may not be valid. In reality a population may be in a state of continual flux, moving from one equilibrium state to another as external conditions vary (Holling 1973). Given our uncertainty over the nature of the catch/effort surface, it is not reasonable to permit efforts to change drastically as this does not permit the population to respond fully to the initially applied effort. However, the cost of obtaining information on the possible equilibrium under a given effort regime obviously has to be weighed against the socioeconomic and the political costs. Because of the uncertainties it would seem highly advisable to adopt management strategies that are conservative; for example, it may not be wise to permit a fishing fleet to grow at a rate faster than it can be reduced [for an economic analysis of the costs of such a policy in the Norwegian purse seiner fleet see Hansen (1979)]. Ideally, the best situation would be one in which acceptable (from the social, economic, and political point of view) perturbations to the system could be made that would increase our understanding of the systems response surface (Walters and Hilborn 1976, 1978).

Attempts to determine equilibrium yields from catch-and-effort data are as likely to be successful as finding the pot of gold at the end of the rainbow. There are two reasons for this: first, as suggested, above the body of ecological literature points to population fluctuations being the result of the interaction of environmental, inter- and intra-specific factors. A single population equilibrium is highly unlikely to exist and models based on such principles may be both unrealistic and misleading. The second reason concerns the information content of the catch-and-effort data. Being extracted from a diversity of sources the reliability of the data must always be suspect. Whereas the data may be sufficiently accurate to reflect gross changes in population size, attempts to extract more subtle information may be attempts to interpret noise as biological variation. This does not, however, mean that optimal management policies cannot be established. What it does mean is that management policy must be adaptive and based on a short-term time horizon (see above) rather than an estimated equilibrium that may be a statistical artifact (Roff and Fairbairn 1980).

Acknowledgments

I am most grateful for useful discussions on the analysis of catch/effort data with Drs J. A. Gulland, D. J. Garrod, and A. T. Pinhorn. Dr G. G. Walter provided useful comments on an earlier draft of this paper. I thank Dr Deriso for providing the Georges Bank Haddock data.

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NOTES

Distinguishing Beaked Redfishes (Deepwater Redfish, *Sebastes mentella* and Labrador Redfish, *S. fasciatus*) by Discriminant Analysis (with Covariance) and Multivariate Analysis of Covariance

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MISRA, R. K., AND I-H. NI. 1983. Distinguishing beaked redfishes (deepwater redfish, *Sebastes mentella* and Labrador redfish, *S. fasciatus*) by discriminant analysis (with covariance) and multivariate analysis of covariance. Can. J. Fish. Aquat. Sci. 40: 1507–1511.

Analysis of morphometric data for differentiating fish species and stocks has frequently been unsatisfactory as a result of sampling bias associated with the varying size of specimens and the large overlapping of characters. These difficulties may be overcome by using a discriminant function with covariance and multivariate analysis of covariance. In a classification study of beaked redfishes, in which the specimens of Labrador redfish (*Sebastes fasciatus*) are relatively smaller than those of deepwater redfish (*S. mentella*), a single character would not separate species, but a compound criterion (discriminant function) of several characters separated the species effectively. A discriminant function with covariance separated species/populations remarkably well and better than one without covariance. Seven morphometric characters were identified as pertinent discriminators between *S. fasciatus* and *S. mentella*. As much as 89% of the total variation in the sample was accounted for by the discriminant function and only 8 out of 198 individuals (4%) were in the zone of uncertainty. It is explained why using a large number of characters in discriminant analysis may not be appropriate for samples of limited sizes. Also, expressing morphometric measurements as ratios, proportions, or percentages of body length may not be an appropriate way of reducing variation owing to size differences.

MISRA, R. K., AND I-H. NI. 1983. Distinguishing beaked redfishes (deepwater redfish, *Sebastes mentella* and Labrador redfish, *S. fasciatus*) by discriminant analysis (with covariance) and multivariate analysis of covariance. Can. J. Fish. Aquat. Sci. 40: 1507–1511.

L'analyse des données morphométriques pour différencier les espèces et les stocks de poisson a souvent été insatisfaisante à cause du biais d'échantillonnage associé avec la variation de la taille des spécimens et l'important chevauchement des caractères. On peut surmonter ces difficultés en utilisant une fonction discriminante avec une covariance et une analyse multifactorielle de la covariance. Dans une étude de classification des sébastes à bec (les spécimens de *Sebastes fasciatus* sont relativement plus petits que ceux de *S. mentella*) un caractère unique ne réussissait pas à séparer les espèces mais un critère composé (fonction discriminante) de plusieurs caractères les différenciait de façon efficace. Une fonction discriminante avec une covariance séparait les espèces et les populations remarquablement bien et mieux qu'une autre sans une covariance. Sept caractères morphométriques ont été identifiés comme discriminateurs appropriés de *S. fasciatus* et *S. mentella*. La fonction discriminante a pu répondre pour 89 % de la variation totale de l'échantillon et seulement 8 spécimens sur 198 (4 %) se classaient dans la zone d'incertitude. On explique pourquoi l'utilisation d'un grand nombre de caractères dans l'analyse discriminante n'est pas toujours indiqué pour des

Printed in Canada (J7171)
Imprimé au Canada (J7171)

échantillons de petite taille. De plus, l'expression des mesures morphométriques comme quotient, proportion ou pourcentage de la longueur du corps ne convient peut-être pas pour réduire la variation attribuable à des différences de taille.

Received December 14, 1982
Accepted May 19, 1983

Reçu le 14 décembre 1982
Accepté le 19 mai 1983

THE effective management of redfish resources in the Northwest Atlantic requires a clear understanding of *Sebastes* species composition and stock units. However, for decades the distinction between deepwater redfish (*S. mentella*) and Labrador redfish (*S. fasciatus*) has not been clear. Although the separation can be made on the basis of the extrinsic gas bladder musculature alone (Ni 1981a), examination of this character is time-consuming and not practical in the field. Ni (1981b) used data on meristic and nominal characters only and reported that discriminant analysis was remarkably effective in separating the two species and for identifying good discriminators for use in the field. However, he did not apply discriminant analysis to morphometric data because the specimens of *S. fasciatus* were smaller than those of *S. mentella* and the range of characters overlapped broadly between groups. This difficulty is frequently encountered in morphological studies of species differentiation and stock discrimination in fish. We believe that use of discriminant function with covariance will overcome this difficulty.

Fisher's discriminant function has been extensively used in applied research (Goldstein and Dillon 1978), because "even when two similar species can be identified with a single measurement, a combined criterion of two or more may increase the separation between them" (Bliss 1970). Multivariate normal distribution is a required condition for Fisher's linear discriminant function (LDF) to yield an optimal assignment rule (Dillon 1979). Performance of LDF in non-normal situations can be very misleading (Lachenbruch et al. 1973; Dillon 1979). Morphometric measurements are taken on "continuous" variables and are far more appropriate for discriminant analysis as multivariate normality is closely approximated by their logarithms (Pimentel 1979, p. 57; Bliss 1967, p. 115). Because individuals vary within populations (e.g. standard length), this warrants adjustment in characters (variates) by covariance for inequalities in the standard length to achieve improved discrimination (Bliss 1970). A valid discriminant analysis must be preceded by a significant difference between population mean vectors (Pimentel 1979). This may be tested by multivariate analysis of covariance (MANCOVA). As far as the authors are aware neither methodology has been used for comparing fish populations, although the utility of ANCOVA at the univariate level has long been recognized (Marr 1955; Royce 1964). Discriminant analysis would be particularly appropriate when the existence of reference samples can be assumed on a basis of an external criterion (Kendall and Stuart 1976), as in this study of redfish data where reference samples were formed on the basis of the extrinsic gas bladder musculature (Ni 1981a).

In this paper, (1) methodologies of MANCOVA and discriminant analysis with covariance are introduced and applied to a classification study of beaked redfishes based on morphometric data. (2) It is pointed out that parsimony in the number of characters to be included in the discriminant analysis is desirable for samples of limited sizes. (3) It is explained why expressing morphometric measurements of characters as ratios, proportions, or percentages of body length may not be an appropriate way of reducing variation owing to size differences. We also discuss intermediate results which are not easily accessible even though these details are often of interest to users.

Materials and methods — Morphometric data on 100 *S. fasciatus* and 100 *S. mentella* specimens described by Ni (1981a, b) were used in the present study. These specimens were separated into the two groups on the basis of the extrinsic gas bladder musculature prior to discriminant analysis. All specimens were frozen after capture and thawed prior to measurement. Twelve morphometric characters were examined (Table 1), most of which were suggested by Barsukov and Zakharov (1972) and Barsukov (1972). Characters were measured with calipers to the nearest 0.1 mm except standard length which was rounded to the nearest 1 mm. Head length and preanal length were measured from the anterior part of upper jaw to the relevant posterior point on a line parallel to the main axis of the fish. Body weight was recorded to the nearest 1 g.

Statistical methodology was organized and the computer program written in FORTRAN by one of us (R.K.M.).

Statistical analysis and results — Although it is often believed that the effect of size differences in population comparisons can be eliminated by expressing measurements as ratios, proportions, or percentages of body length (e.g. Casselman et al. 1981), this procedure has long been criticized (Marr 1955; Royce 1964; Blackith and Reyment 1971). The following demonstrates that this may not be an appropriate procedure: Consider, e.g. two variables X (body size such as standard length) and Y (a morphometric character) related by an equation of simple allometry,

$$(1)\quad Y = aX^b$$

where a and b are constants. Equation (1) shows that Y is functionally related to X and requires adjustment in its value for the effect of X. Rearranging, $Y/X = aX^{(b-1)}$ which is of the same form as (1). Thus, the ratio (or percentage) Y/X is affected by X just as Y itself is, barring the special case when $b = 1$. In fact, a statistical analysis of Y/X would very likely be more questionable than the analysis of Y itself, because, for example, ratios have unusual distributions and are subject to various errors (Pimental 1979, p. 60). The argument against the appropriateness of analyzing ratio data would always hold when X and Y are correlated, even if not related by allometry. For example, a simple linear regression $Y = a + bX$ for Y leads to the equation $Y/X = a/X + b$ which shows that the ratio is still not independent of X.

TABLE 1. Means and ranges of body weight (g) and 11 morphometric characters (mm) Y_i ($i = 1, \ldots 12$) for *S. mentella* ($n = 97$) and *S. fasciatus* ($n = 99$). All measurements were transformed to common logarithms.

Character (Y_i)	Character description	*S. mentella*		*S. fasciatus*	
		Mean	Range	Mean	Range
1	Body weight	2.7000	2.1703−3.2423	2.2324	2.0374−2.6830
2[a]	Head length	2.0011	1.8325−2.1772	1.8211	1.7634−1.9685
3	Snout length	1.3564	1.1584−1.5428	1.1586	1.0682−1.3365
4	Inter orbital width	1.2421	1.0775−1.4099	1.0486	0.9638−1.2529
5[a]	Preanal length	2.2466	2.0846−2.4190	2.0991	2.0158−2.2480
6[a]	Pectoral fin base	1.3460	1.1790−1.5198	1.2184	1.1335−1.3856
7[a]	Anal fin base	1.6124	1.4330−1.7528	1.4438	1.3522−1.6107
8[a]	Length of longest pelvic ray	1.6723	1.4914−1.8156	1.5486	1.4265−1.6776
9[a]	Length of longest pectoral ray	1.8380	1.6484−1.9845	1.6712	1.6085−1.8312
10	Width of caudal peduncle	1.3522	1.1875−1.5340	1.2103	1.1335−1.3579
11[a]	Dorsal length of caudal peduncle	1.5954	1.3324−1.7679	1.4351	1.3263−1.5888
12	Standard length	2.4238	2.2742−2.5763	2.2725	2.2041−2.4133

[a]Number indicates the effective discriminator with standard length (Y_{12}) as covariate.

All measurements were transformed to common logarithms for MANCOVA and discriminant analysis for the following reasons. (1) Multivariate normality is usually more closely approximated by logarithms than by the original variables (Pimentel 1979, p. 57; Bliss 1967, p. 115). (2) MANCOVA adjustments generally assume linear relationships and this assumption is also made in the present analysis. Logarithmic transformation should satisfy a test of linearity (Pimentel 1979, p. 60 and 182). (3) The convention is to use common logarithms (Pimentel 1979, p. 57). Only complete specimens, i.e. specimens for which all 12 measurements were available, were used in statistical analyses because "missing observations virtually destroy morphometrics" (Pimentel 1979, p. 191). Samples from *S. mentella* and *S. fasciatus* had 97 and 99 complete specimens, respectively. Morphometric characters listed were designated Y_i, $i = 1, 2, \ldots, 12$ (Table 1).

"A series of univariate statistical analyses carried out separately for each of the variables, is, in general, not adequate as it ignores the correlations among variables" (Kshirsagar 1972). Following Bliss (1970, p. 329 and 332), the following was noted: ranges of characters (Table 1) overlapped between species, from 39% (Y_2) to 60% (Y_{11}) in *S. mentella* and from 61% (Y_4) to 98% (Y_{11}) in *S. fasciatus*. With these large overlaps no single character would separate species effectively. The probability of misclassification based on Lubischew's coefficient of separation was large, varying from 7.5% (for Y_6) to 18.2% (for Y_9). Yet univariate analysis of variance (ANOVA) to test null hypotheses of equality of means indicated that the difference between species in means was highly significant ($P < 0.001$) for each character. It was, therefore, desirable to find a compound criterion (discriminant function) of characters which would make identification possible from several measurements.

Discriminant analysis is valid only if populations differ significantly in their means (Pimentel 1979, p. 188). Discriminant analysis was therefore preceded by MANCOVA with standard length (Y_{12}) as covariate. In the general linear model of MANCOVA the within-sample linear regression of each variate Y_i on the covariate is incorporated and sample mean vectors $\mathbf{Y}$ are thereby adjusted for inequalities in standard length (Bliss 1970; Morrison 1976). Large overlaps of 46% in *S. mentella* and 67% in *S. fasciatus* in the ranges of Y_{12} (Table 1) and its inadequacy to discriminate effectively between the two species supported the use of standard length as a covariate (Snedecor and Cochran 1967, p. 430). MANCOVA assumes that populations do not differ in their regression model and hence uses the matrix B of computed regression coefficients from "within-sample" sums of squares and products (SS and SP) matrices (Morrison 1976).

The null hypothesis of no difference between species in slopes (weighted by SS of the covariate) of individual variates was, therefore, tested and accepted ($P > 0.05$). When the combined slope of a Y_i differs significantly from zero, the residual variation in Y_i about each sample regression will be less than that around the respective means of individual samples with the covariate ignored, thereby leading to a more effective comparison of means and discriminant function based on the covariance procedure. The null hypothesis $B = 0$ of no linear regression of variates on the covariate was tested by the union intersection procedure. The test statistic Θ was 0.9889 with values 1, 4.5, and 90.5 of parameters s, m, and n, respectively (Morrison 1976, Sect. 5.4), leading to the rejection of the null hypothesis ($P < 0.001$). The null hypothesis of equal vectors of adjusted means was tested next (Morrison 1976, Sect. 5.4). The test statistic Θ was 0.7243 with the same values of s, m, and n. The null hypothesis was rejected in favor of the conclusion that the two species differ in mean values of one or more variates independent of the

difference between them in standard length.

It was considered desirable to investigate which of the 11 variates, if any, did not contribute to the difference between species in the MANCOVA, with the aim of omitting them from discriminant analysis. Discriminant analysis has a close analogy to multiple regression with many stages of calculation parallel to those for a multiple regression but with X and Y reversed (Bliss 1970;Kshirsagar 1972). The expected value of R^2, coefficient of multiple correlation squared, is proportional to the number of variates (Morrison 1976, p. 108), implying that for samples of limited sizes a large number of characters would artificially inflate the discriminatory power of the discriminant function. "Far too many studies of multiple regression have been carried out in biology using few observations and many different predictor variables" (Sokal and Rohlf 1981, p. 670). A smaller number of characters also makes discriminant function more convenient in field studies. Furthermore, omitting variates with nonsignificant coefficients increases the stability of the discriminant function (Bliss, 1970, Sect. 18.3). Following Morrison (1976, Sect. 5.5), 95% simultaneous confidence intervals for characters were estimated. The hypothesis of no significant difference between two species in the adjusted means of Y_3 (snout length) and Y_{10} (width of caudal peduncle) was accepted, as their confidence intervals included zero. Discriminant analysis was therefore done for variates Y_1, Y_2, Y_4, Y_5, Y_6, Y_7, Y_8, Y_9, and Y_{11} only, with Y_{12} as the covariate.

The discriminant analysis methodology used here (mainly from Bliss 1970, Chap. 18 and 20) combines discriminant analysis with analysis of covariance by adjusting variates by means of their within-sample regressions on the covariates and then finding a compound response (Z) of adjusted variates which would measure best the difference between two species. Species were qualified by values +1 and −1 of "dummy variate" X and discriminant coefficients computed so as to maximize the ratio of Z to its standard error (SE). This Z may be expressed as

$$Z = \sum_i L_i Y_i - \sum_i L_i b_{i.12}\, d,\ i = 1, 2, 4, 5, 6, 7, 8, 9, 11$$

where L_i is discriminant coefficient, $b_{i.12}$ is within-sample coefficient of regression of Y_i on Y_{12}, and d is the difference between the observed value and a selected level of the covariate Y_{12}, the selected level in this analysis being its overall mean (Bliss 1970). For the redfish data computed $Z = 10.5866 + 0.8935Y_1 - 9.6952Y_2 - 1.5965Y_4 + 5.7151Y_5 + 12.3990Y_6 - 4.7132Y_7 + 6.5272Y_8 - 7.7912Y_9 - 1.3918Y_{11} - 4.5100Y_{12}$. Simultaneous equations determining L_i (Bliss 1970, p. 335) were based on "total" SS and SP to facilitate the ANOVA of Z in terms of X. ANOVA showed that 89% of the total SS in X was attributable to the discriminant function. In an attempt to reduce the number of variates further, this ANOVA was extended to test the significance of each discriminant coefficient the same way as a partial regression coefficient is tested (Bliss 1970). The null hypothesis that each L_i has true or population value of zero was accepted ($P > 0.05$) for Y_1 ($F = 1.36$), Y_4 ($F = 1.89$), and Y_{11} ($F = 3.55$), each F with degrees of freedom (df) = 1,185, and rejected for every other variate. The following were noted (Bliss 1970, Sect. 18.3): (1) If coefficients for two or more variates are nonsignificant, the one with the smallest F is omitted first. Omitting a variate with a nonsignificant coefficient reduces the error of the remaining recomputed coefficients, especially if the variate is highly correlated with one or more of the other variates. Stability of the discriminant function based on remaining variates is also increased by its omission. For the redfish data paired within-sample coefficients of correlation were all high (in the range of 0.76−0.98). (2) Deletion of variates is continued, one at a time and starting with the one which yields smallest F value, until each remaining variable has a significant effect. Following this procedure, the discriminant function was recomputed with Y_1 (body weight) omitted. The recomputed value of the discriminant coefficient for Y_4 was still nonsignificant. Therefore, the discriminant function was recomputed with Y_4 (interorbital width) omitted. As discriminant coefficients of all the remaining variates were then significant ($P < 0.05$), computation was stopped at this point. ANOVA of the discriminant function for the reduced set of variates indicated that percentage of the total SS in X attributable to the discriminant function was still the same, viz. 89%. Thus, it was sufficient to use seven variates in the discriminant function. It was, however, noted that the combined effect of all partial regression coefficients cannot be partitioned orthogonally when the variates are correlated with one another (Bliss 1970, Sect. 18.3). Interpretations based on individual discriminant coefficients may, therefore, be of restricted scope. Discriminant analysis use (rather than removes) intercorrelations among variates (Pimentel 1979).

For discriminant analysis with seven variates Y_2, Y_5, Y_6, Y_7, Y_8, Y_9, and Y_{11} and the covariate Y_{12}, the number of "complete" specimens was 99 in each sample. The discriminant function computed was $Z = 7.0682 - 10.2039Y_2 + 5.6028Y_5 + 12.8670Y_6 - 5.0213Y_7 + 7.3811Y_8 - 8.2966Y_9 - 1.5160Y_{11} - 3.0098Y_{12}$. A larger discriminant coefficient does not necessarily indicate a measure of greater importance than a smaller discriminant coefficient (Bliss 1970). ANOVA of discriminant coefficients by the partial regression approach indicated that characters (Table 1) did not contribute equally and were, in fact, placed in the following order of decreasing importance: pectoral fin base (Y_6 with $F = 115.94$), length of longest pelvic ray (Y_8), head length (Y_2), length of longest pectoral ray (Y_9), anal fin base (Y_7), preanal length (Y_5), and dorsal length of caudal peduncle (Y_{11} with $F = 4.26$), each F with df = 1,189. Variance of a single Z was estimated as 0.086105. When the discriminant function was computed with Y_{12} (standard length) included as an additional discriminator (rather than as a covariate), variance of a single Z was 0.103184 which is as much as 20% higher than 0.086105. This indicated, in yet another way, that a discriminant function with covariance provided more effective discrimination than one without it. Mean Z values were −4.1697 and −2.77552 for *S. mentella* and *S. fasciatus*, respectively. Difference between these means was highly significant ($P < 0.001$). The zone of uncertainty or wrong identifications of individuals at each end (at $P = 0.05$) was small viz. −3.6530 to −3.2883. Only 8 out of 198 individuals (i.e. 4%) were in this zone of uncertainty.

Acknowledgments — We are grateful to Mr L. S. Parsons and

Mr E. M. LeGrow for the privilege of using previously collected data. Dr G. R. Lilly and Mr B. Gellately kindly reviewed the manuscript.

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Mortality Due to Infectious Hematopoietic Necrosis of Sockeye Salmon (*Oncorhynchus nerka*) Fry in Streamside Egg Incubation Boxes

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MULCAHY, D., R. PASCHO, AND C. K. JENES. 1983. Mortality due to infectious hematopoietic necrosis of sockeye salmon (*Oncorhynchus nerka*) fry in streamside egg incubation boxes. Can. J. Fish. Aquat. Sci. 40: 1511–1516.

Infectious hematopoietic necrosis virus caused mortality of sockeye salmon (*Oncorhynchus nerka*) in streamside egg incubation boxes. Virus was not detectable in eggs or alevins; its first isolation coincided with the appearance of dead fish in a trap on the outflow from the box. Mortality due to the virus did not occur in every egg box studied. However, when fry from the boxes were held in the laboratory, epizootics began as much as 3 wk later, with total mortality exceeding 90%. More than 96% of the dead fry had titers exceeding 10^5 plaque-forming units per gram. The peak incidence of virus in fry migrating in the river coincided with the arrival of hatchery-produced fry, although some fry believed to have been produced by natural spawning were also infected.

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Le virus de la nécrose hématopoïétique infectieuse a causé la mort de saumons nerka (*Oncorhynchus nerka*) dans des boîtes d'incubation placés dans un cours d'eau. Le virus n'a pas été détecté dans les oeufs ou les alevins; il a été isolé pour la première fois en même temps qu'apparurent des poissons morts dans une trappe à la sortie des boîtes d'incubation. Ces mortalités ne se sont pas produites dans toutes les boîtes étudiées. Cependant, quand les alevins provenant des boîtes furent maintenus en laboratoire, des épizooties se déclenchèrent

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Printed in Canada (J6999)
Imprimé au Canada (J6999)

jusqu'à 3 semaines après, les mortalités totales dépassant 90 %. Plus de 96 % des alevins morts avaient des titres dépassant 10^5 unités formant des plages par gramme. Le maximum d'incidence du virus chez des alevins migrant en rivière coïncida avec l'arrivée d'alevins de pisciculture, bien que des alevins que l'on croit avoir été produits par reproduction naturelle, fussent également infectés.

Received July 8, 1982
Accepted June 2, 1983

Reçu le 8 juillet 1982
Accepté le 2 juin 1983

INFECTIOUS hematopoietic necrosis virus (IHNV) has been found in every population of sockeye salmon (*Oncorhynchus nerka*) that has been examined (Guenther et al. 1959; Amend and Wood 1972; Grischkowsky and Amend 1976) and is a major limiting factor in hatchery culture of this species (Grischkowsky 1981). As an alternative to standard hatcheries, egg incubation boxes are an inexpensive, relatively simple means of increasing the survival rate of salmon eggs and alevins compared to natural spawning, by protecting the eggs from predation, dewatering, and flushing of eggs from the gravel. Salmon eggs are fertilized, washed, disinfected, and placed over the gravel in the boxes. After hatching and early development, the fry leave the boxes of their own volition. Mortality due to IHNV in sockeye salmon fry in these boxes has been observed (Mulcahy and Bauersfeld 1983) but has not been characterized because fry produced in egg incubation boxes are rarely retained for extended observation of possible mortality. We studied IHNV in sockeye salmon fry hatched in egg incubation boxes for two seasons, and herein describe the incidence of disease among fry in a group of boxes, kinetics of the losses due to the disease, quantification of levels of virus associated with loss, and occurrence of the virus in migrating fry.

Materials and methods — Sockeye salmon eggs were taken in the 1979 and 1980 brood years from a population in the Cedar River, Washington, which has a high incidence of IHN virus in the spawning adults and a history of the disease in fry. Eggs were collected in late September through October. After fertilization, they were rinsed with water and treated for 10 min with 100 mg/L iodophore with 0.5% sodium bicarbonate. About one million eggs per box were spread evenly on trays placed over the surface of the gravel. Fungus infections of the eggs were controlled with weekly malachite green treatments (2 mg/L for 1 h). The eggs began to hatch in late January and fry began to emerge near the end of February. After emergence from the boxes, migration time of the fry to the nursery lake was as little as 6 h.

Egg incubation boxes — The streamside egg incubation boxes were gravel-filled plywood boxes, 2.5 × 1.25 × 1.25 m (Allen and Cowan 1978). They each received spring water at 6–8°C at a rate of 190 L/min. A total of 11 boxes were located about 32 km upstream from the nursery lake used by the sockeye salmon fry. Before fry emergence began, wire box traps were placed on the outlets of some of the incubation boxes to intercept all emergent fry.

Egg, alevin, and fry samples — Eyed eggs, alevins, and emergent fry were collected at intervals from each box studied during the 1979 brood year. Only emergent fry from the 1980 brood year were tested. Five eggs or fry were placed in sterile tubes on ice and brought to the laboratory. Fry migrating to the nursery lake from the egg incubation boxes and from natural spawning were captured with a fyke-net near the mouth of the river. The source of these fry could not be identified. To monitor postemergent fry losses, about 200 fry in 1980 and about 500 fry in 1981 were taken from each trap on the boxes studied at or after the peak of emergence. In the laboratory, all dead or dying fry were removed and the remainder were placed in 30-L tanks with 10°C running water. Dead fry were removed daily for viral titration.

Viral titration — Virus in the fry was titrated by the plaquing technique, using the epithelioma papillosum cyprini cell line (Burke and Mulcahy 1980). Samples were processed within 24 h after collection as previously described (Mulcahy et al. 1983). Viral titers were determined as plaque-forming units per gram (pfu/g) of fry, and mean viral titers were calculated after transformation of individual titers to logarithmic ($\log_{10}$) values.

Results — No IHNV was detected in eggs and alevins from the 1979 brood year sampled from streamside egg incubation boxes (Fig. 1). The virus was first found when fry began emerging from the gravel in Box A and coincided with the first appearance of dead and moribund fry in the trap, indicating the occurrence of an epizootic. Both the incidence of virus isolation and mean viral titer rose rapidly as emergence progressed.

Dead fry were rarely observed in the trap on Box B. No testing was done until moribund fry were observed during the last sampling period. Then, the incidence of IHNV was 75%, but the mean titer was relatively low suggesting that the epizootic was just beginning in that box (Fig. 1).

To determine the extent of fry mortality due to IHNV in the egg incubation boxes, we sampled emergent fry from the 11 boxes containing eggs from the 1979 brood year. Fish could not always be captured from every box on each sample day. Fry from 5 of the 11 boxes were infected with IHNV, usually at a high mean titer (Table 1). Infected fry may not have been detected in boxes from which few fry were sampled. When masses of affected fish were netted, there was a noticeable iridescent red, blue, and green pigmentation on the sides of affected fish in contrast to the silver coloration of unaffected fish. This iridescence was much less noticeable when one examined individual fish.

Unless trapped for sampling, emergent fry entered the river almost immediately and were lost to detailed observation. In both years of the study, groups of emergent fry were removed from the traps below some boxes and held in the laboratory for evaluation of postemergence mortality. Mortality due to

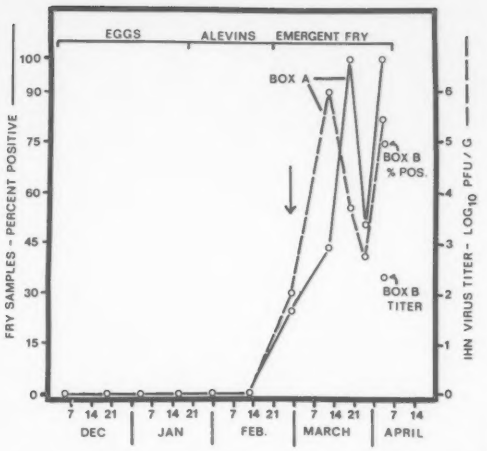

FIG. 1. Occurrence (solid line) and mean titer (broken line) of IHNV in sockeye salmon eggs, alevins, and emerging fry sampled from egg Box A in the 1979 brood year. Arrow indicates the onset of mortality. Viral incidence and mean titer are also given for a single sample of emergent fry from egg Box B.

IHNV exceeded 90% in all four groups of fry held in the laboratory for extended observation (Fig. 2). Mortality began an average of 133 d after fertilization (Table 2). In one box (Box B), mortality occurred in fry held in the laboratory about 6 d before dead fish were seen in the trap on the box. In the other boxes mortality of fry in the laboratory occurred 6–21 d after mortality began in the boxes. Typically, epizootics began suddenly and most of the fish died within 3 wk. Individual fish often died within 60–90 min of the onset of signs.

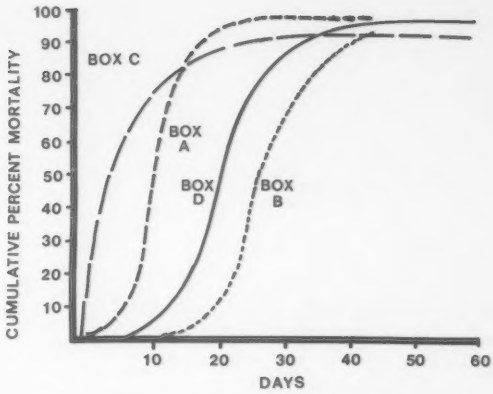

FIG. 2. Mortality curves for postemergent fry taken from egg incubation boxes in the 1979 (Boxes A and B) and 1980 (Boxes C and D) brood years and held in the laboratory for extended observation. All dead or dying fish were removed on arrival in the laboratory, before the extended observation period began.

A severe and rapid epizootic occurred in the fry removed from Box C, with 75% of the fry dying in the first 10 d.

In 1980, fry taken from egg Boxes A and B weighed less than the fry held in the laboratory (Table 3). No differences were seen in Boxes C and D, sampled in 1981. The incidence of virus was usually lower in fry taken from the boxes than in those held in the laboratory, reflecting the practice of taking asymptomatic fry from the boxes when dead fry were not present in sufficient numbers. Typically, once the viral epizootic started, IHNV was isolated from virtually all samples. Because only dead fry were tested from the groups held in the

TABLE 1. Incidence of IHNV (as percent positive of all fry sampled) in 1979 brood year in emergent sockeye salmon fry removed from egg incubation boxes or from traps placed on the boxes. Five fry from each box were sampled whenever possible. All previous samplings of eggs or alevins were negative. Mean viral titers (shown in parentheses) are pfu/g of whole fish. Boxes C and D not studied. (nd = not determined.)

	Date sampled in 1980				
Box	Feb. 28	March 13	March 20	March 27	April 3
A	25 (1.0×10^2)	100 (1.5×10^6)	100 (5.2×10^3)	50 (5.2×10^2)	100 (2.9×10^5)
B	nd	nd	nd	nd	75 (3.5×10^2)
E	0	0	0	0	nd
F	nd	nd	nd	nd	50 (3.9×10^2)
G	0	0	0	25 (1.3×10^5)	nd
H	nd	nd	0	nd	nd
I	nd	50 (1.9×10^5)	100 (5.5×10^5)	nd	nd
J	nd	0	nd	0	nd
K	nd	nd	0	0	0
L	nd	nd	nd	nd	0
M	nd	nd	0	nd	nd

TABLE 2. Timing of events and summary of IHN epizootics in sockeye salmon fry in egg incubation boxes and in fry removed to the laboratory for extended observation.

Box	Date eggs fertilized	Date mortality began	Days from fertilization to onset of mortality (no.)	Fry brought to lab (no.)	Cumulative mortality in lab (%)
A	Oct. 19, 1979	Feb. 28, 1980	132	164	98
B	Nov. 19, 1979	April 3, 1980	135	279	94
C	Oct. 20, 1980	Feb. 20, 1981	123	555	92
D	Oct. 15, 1980	March 5, 1981	141	449	96

TABLE 3. Results of viral testing of sockeye salmon fry emerging from streamside egg incubation boxes, fry held in the laboratory, and migrating fry fyke-netted at the mouth of the Cedar River.

Year	Box	Location	Fish weighed (no.)	Mean weight (g)	Fish or pools processed for virus isolation (no.)	Positive (%)	Mean viral titer (pfu/g)
1980[a]	A	Egg box	88	0.16	20	70	4.68×10^{4}
		Lab	115	0.20	115	99	5.87×10^{7}
	B	Egg box	20	0.16	4	75	6.63×10^{4}
		Lab	35	0.24	35	97	1.99×10^{7}
		River mouth[b]	298	0.19	298	7	4.01×10^{3}
1981[c]	C	Egg box	120	0.22	24	100	2.25×10^{7}
		Lab	1	0.22	1	100	6.75×10^{6}
	D	Egg box	111	0.18	22	14	5.93×10^{5}
		Lab	15	0.18	5	100	7.09×10^{7}

[a]1979 brood year.
[b]Fry fyke-netted at mouth of river, originating from both egg boxes and natural spawning.
[c]1980 brood year.

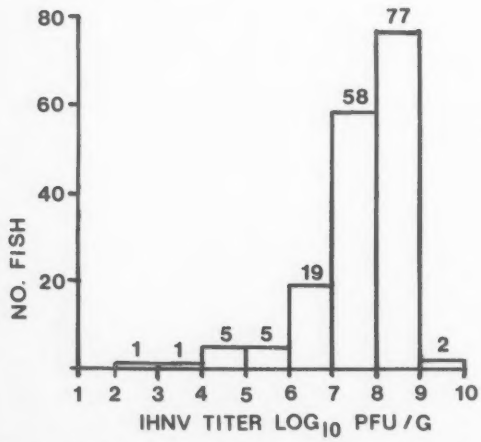

FIG. 3. IHNV titer distributions from 168 dead sockeye salmon fry or fry pools from egg incubation boxes or from fry held in the laboratory. Mean titer was 4.84×10^{7} pfu/g.

laboratory, the percent incidence was extremely high. For the same reasons, the mean viral titers obtained from fry taken from the boxes were generally higher than those from the fry held in the laboratory (Table 3). After IHNV was first identified in any group of sockeye salmon fry in these studies, almost every dead fish had extremely high levels of virus, sufficient to cause death (Fig. 3).

Sockeye salmon fry produced in egg boxes and by natural spawning were obtained by fyke-netting near the mouth of the Cedar River. A low mean viral titer was detected in 7% of the nearly 300 netted fry examined (Table 3). The highest incidence and mean titer coincided with the peak of the migration of the fry produced in the egg boxes (Fig. 4). Both the incidence and mean titer fluctuated greatly during the migration period. Two sets of samples were partially ruined when an incubator malfunctioned but a visual examination indicated that even higher incidences and mean titers probably occurred in early March. Fry captured after April 1 were most likely produced from natural spawning but could not be definitely distinguished from those produced in egg boxes.

Discussion — Although vertical transmission of IHNV is believed to be egg-associated, virus cannot be isolated from incubating eggs or newly hatched alevins in the absence of the acute phase of the disease. Possibly, the virus is associated with the tissue debris removed by centrifugation following tissue homogenization. The first isolation of IHNV in one of the boxes most closely studied coincided with the appearance of dead fry in the trap, indicating that the virus appears rapidly. Attempts to determine by random sampling if a group of apparently normal sockeye fry are infected with IHNV are probably futile unless an epizootic has begun.

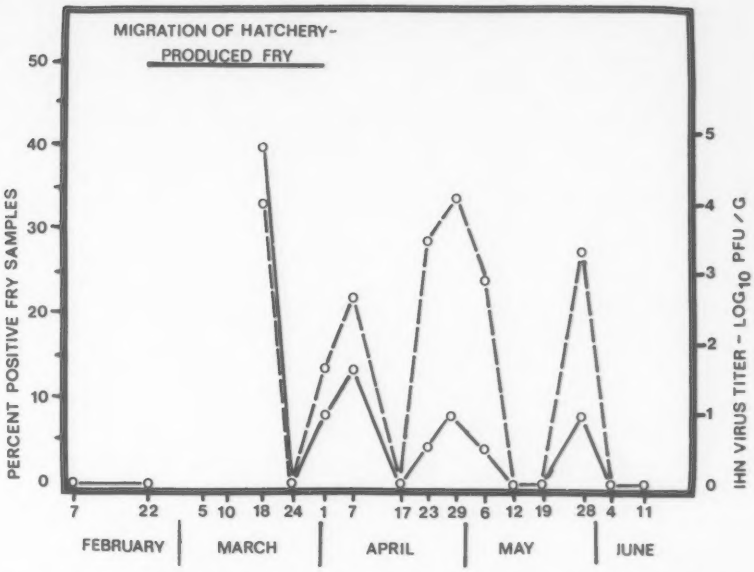

FIG. 4. Occurrence (solid line) and mean viral titer (broken line) of IHNV in migrating sockeye salmon fry fyke-netted near the mouth of the Cedar River, 1980. Fry produced from both natural spawning and egg incubation boxes were included in the sample, but could not be distinguished. Samples collected on 2 days in early March were lost as a result of incubator failure.

As judged by the high incidences and titers found in fry removed from the boxes, IHNV can be as severe a problem in sockeye salmon hatched in egg incubation boxes as it is in fish reared at traditional hatcheries. However, because extended rearing of hatched fry is usually not practiced with such boxes, accurate death rates and mortality figures are not obtainable. Retention of groups of fry for postemergence observation offers an indirect method of measurement of mortality, although conditions in the laboratory differ from those in the wild.

The IHNV was not demonstrated in some boxes — perhaps because sampling was inadequate or there was less mortality (or none) in those boxes. The possible absence of epizootics in these boxes is of interest, as almost all of the adult females in this population were IHNV carriers. Because conditions in all the boxes were similar and the boxes had a common water supply, the only significant difference was which groups of females supplied eggs for each box. The level of virus in ovarian fluids varies greatly from fish to fish in this population (Mulcahy et al. 1983). Study of this factor may offer an explanation for the occurrence of epizootics in some boxes but not in others.

In groups of fish removed from the boxes and held in the laboratory, the death rates were high, 90% mortality typically occurring within 20–30 d after the onset. These rates resemble those reported for sockeye salmon reared in a hatchery (Watson 1953; Watson et al. 1954). Once IHNV is detected in dead fry, practically all subsequent mortality is due to the virus disease, as judged by the high incidences and viral titers in dead fry. Of the viral titers from 168 samples (Fig. 3), 96% exceeded 10^5 pfu/g — the level generally accepted as the minimum associated with death due to virus infection (McDaniel 1979).

Large groups of fry were not retained from all boxes for the extended observation necessary to reveal postemergent viral epizootics, and adequate numbers of fry from each box could not always be caught. For these reasons, it is not possible to determine accurately the total mortality due to IHNV in this facility. However, the large-scale mortality seen in the fry held in the laboratory suggests that the losses are very high.

Acknowledgments — We thank Kevin Bauersfeld, Washington Department of Fisheries, for access to the egg incubation boxes; and Asko Hemmalaya, Fisheries Research Institute, University of Washington, for supplying the fyke-netted fry.

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Bottlenose Dolphins, *Tursiops truncatus*, Can Detect Oil

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GERACI, J. R., D. J. ST. AUBIN, AND R. J. REISMAN. 1983. Bottlenose dolphins, *Tursiops truncatus*, can detect oil. Can. J. Fish. Aquat. Sci. 40: 1516–1522.

Two trained bottlenose dolphins, *Tursiops truncatus*, were tested for their ability to detect visually 12 different oils and 22 oil mixtures confined at the surface in small cylinders. Detection thresholds were established in tests using progressively lighter substances. The animals detected 6-mm slicks of crude, residual, and refined motor oils, and diesel slicks thicker than 17 mm. They could not detect 6-mm thicknesses of leaded gasoline or transparent mineral oil. One dolphin's ability to detect oil improved with experience. While blindfolded, one dolphin could detect 12-mm-thick samples of two crude oils, Bunker C and mineral oil, but only when the latter two were churned and contained air bubbles. We conclude that dolphins detect the thicker concentrations of oil that occur near the source of an oceanic spill, but not lightly colored or refined products that tend to disperse into thin films.

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Nous avons étudié chez deux dauphins à gros nez, *Tursiops truncatus*, dressés la capacité de déceler visuellement 12 différentes huiles et 22 mélanges d'huile gardés à la surface dans de petits cylindres. Les seuils de détection ont été déterminés à l'aide de tests avec des substances progressivement plus légères. Les animaux ont pu détecter des nappes de 6 mm de pétrole brut, de résidu de distillation et d'huiles moteur raffinées et des nappes de diésel supérieures à 17 mm. Ils n'ont cependant pu trouver des nappes de 6 mm d'essence au plomb et d'huile minérale transparente. La capacité d'un des dauphins s'est améliorée avec l'expérience. Les yeux bandés, l'un d'eux pouvait déceler la présence d'échantillons de deux bruts, soit le Bunker C et l'huile minérale, de 12 mm d'épaisseur, mais seulement quand ils étaient brassés et contenaient des bulles d'air. Nous en avons conclu que les dauphins pouvaient localiser les concentrations épaisses de pétrole, présentes près des sources de déversement en haute mer, mais non les produits légèrement colorés ou raffinés qui ont tendance à se disperser en films minces.

Received January 11, 1983
Accepted May 31, 1983

Reçu le 11 janvier 1983
Accepté le 31 mai 1983

WHALES and dolphins have not been observed fouled with oil. Perhaps their smooth skin does not allow oil to adhere as it does to the pelage of fur-bearing mammals (Baker et al. 1981; Brownell and LeBoeuf 1971; Davis and Anderson 1976). Alternatively, cetaceans may be able to detect oil and avoid it by using their acute visual and auditory senses (Pepper et al.

Printed in Canada (J7197)
Imprimé au Canada (J7197)

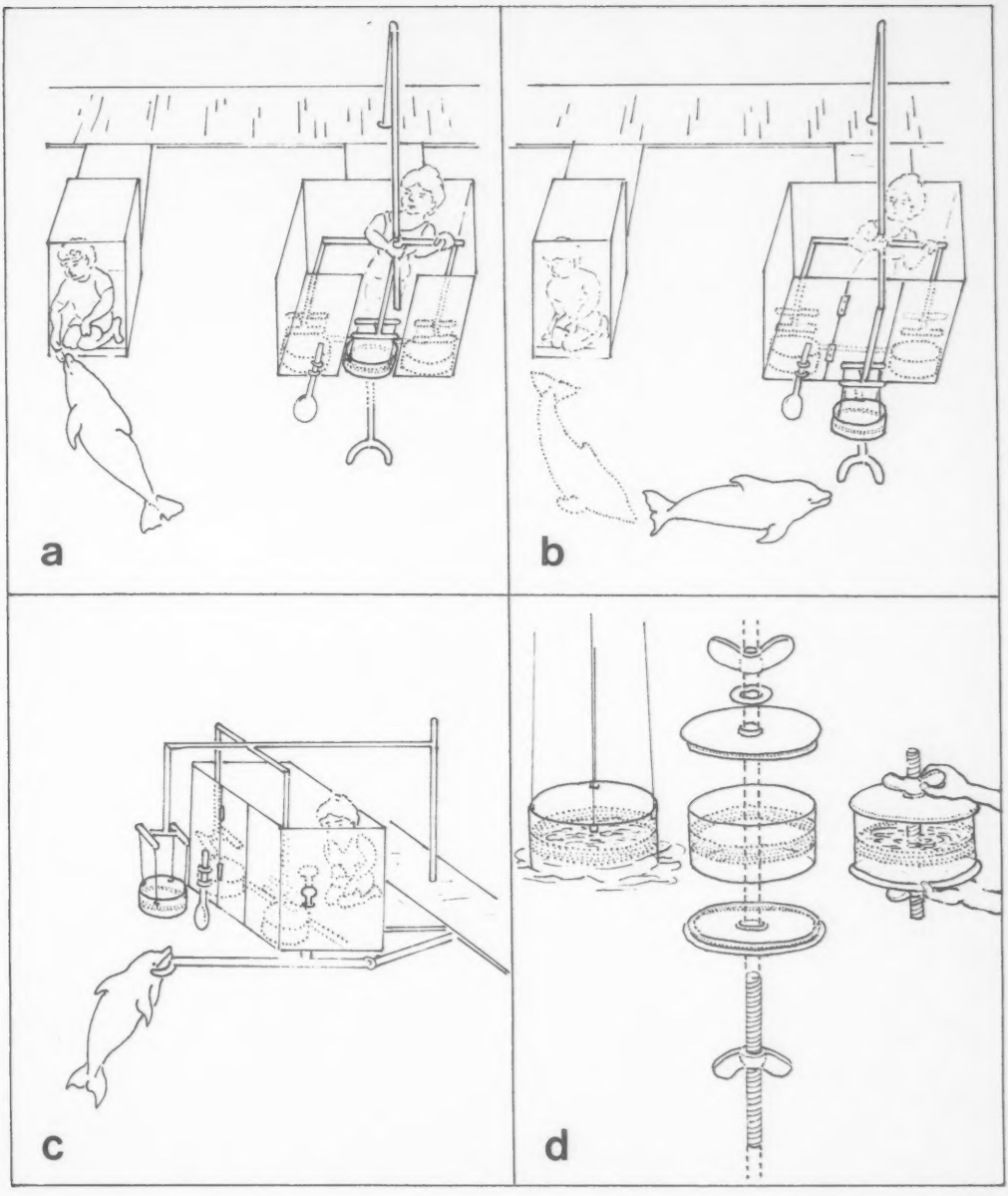

FIG. 1. (a) The trainer calls the animal to the resting dock while an examiner prepares up to three test cylinders in a canal concealed within the trial dock. (b) On command, the dolphin swims to the trial dock, stations on a stirrup, and (c) examines the contents of the cylinder. (d) To retrieve the compounds at the end of each series, the ends of the cylinder were capped so that the entire assembly and its contents could be removed.

TABLE 1. Identification and source of samples used in the oil detection study.

	Source
Crude oils	
Inter-Provincial	Shell Refinery, Oakville, Ont.
West Texas	Shell Refinery, Oakville, Ont.
Unidentified	Brokerage warehouse, Miami, FL
Residual oils	
Bunker C	Belcher Oil Co., Port Everglades, FL
Beach tar	Florida Keys
Refined motor oils	
Quaker SAE30	Quaker State Oil Refining Co., Oil City, PA
Kendall SAE20	Kendall Refining Co., (Division of Witco Chemical Co.), Bradford, PA
Evinrude 2-cycle (50/l)	Evinrude Corp., Beloit, WI
Mineral oil	
Adams Heavy White Mineral Oil (Stock #118)	Adams Laboratories Div., Miami, FL
Refined fuels	
Diesel #2 (Lots A and B)	American Petrofina Marketing Inc., Port Arthur, TX
Regular gasoline (leaded)	Texas Oil Corp.

1972; Herman et al. 1975; Murchison 1980; Nachtigall 1980). As an approach to this question, we sought to determine whether trained bottlenose dolphins, *Tursiops truncatus*, could detect crude oil and refined petroleum products, within a controlled experimental setting.

Materials and methods — The study was conducted at the Institute for Delphinid Research on Grassy Key, Florida. We used captive-born dolphins, a 5-yr-old male and a 6-yr-old female weighing 135 and 158 kg, respectively, at the start of the study in February 1980. The dolphins were selected because both were experienced in visual discrimination studies. They were in good health, as judged from behavior, appetite, physical condition, and blood analyses. The female was removed from the study in June 1981 because of eye injury unrelated to the experiment.

The dolphins were maintained in a wire fence enclosure in a lagoon along the Gulf of Mexico, with ambient water temperature and salinity ranging between 11 and 27°C, and 36 and 42‰, respectively. They were fed rainbow smelt, *Osmarus mordax*, and Atlantic herring, *Clupea harengus* as rewards during the detection tests, and also at the end of each day, to make up the balance of their prescribed daily ration of 5.8–7.9 kg. Feeding rates were calculated to be 60–70 kcal·d^{-1}·kg^{-1} body weight (0.25–0.29 J·kg^{-1} body weight).

Study plan and testing procedure — Each dolphin was trained to position itself on a fixed underwater station at a depth of 1 m, and view a short open-ended cylinder confining various materials and objects at the surface. The animal would leave the station to press a paddle after detecting a substance within the cylinder ("go" response), or otherwise remain stationary for 5 s ("no-go") (Schusterman 1980). We shaped the behavior using solid objects, such as wood, plastic, and styrofoam, which initially filled the entire area within the cylinder. After the animal mastered the technique, these materials were gradually replaced with oil, until the cylinder contained only oil. Once trained to detect solid objects, it took only 3 d for the dolphins to respond to the presence of oil alone. In addition to the visual discriminatory trials, the male dolphin was required to perform the same tasks while blindfolded.

The study area consisted of a rectangular pen with one wall of crushed coral and three of wire fencing. It was 49 m long, 12.8 m wide, with an average water depth of 4–5 m, depending on the tide. Two small square platforms placed 5.7 m apart were hinged to a dock which ran along one side of the pen. The platforms floated on styrofoam blocks so that they maintained a constant level in water. One platform, the resting dock, was occupied by a trainer who fed the animals and interacted with them between tests (Fig. 1a).

The second platform served as the trial dock, where an examiner prepared and deployed cylinders containing samples to be viewed by a dolphin. The examiner was hidden from the trainer and the dolphin by a roof, two solid side panels, and a front panel with 1-way windows allowing a view to the outside. Cylinders were deployed and retrieved through a small door that opened into a 3.1 × 0.6 m canal in the floor along the front of the trial dock (Fig. 1a).

The sound of the door closing announced the beginning of each test. This was the cue for the trainer at the resting dock to broadcast a 200 Hz tone using a modified model EV-04 miniature organ (Bambino Inc., Los Angeles, CA), fed through an MPA-20 amplifier (Radio Shack Inc., Fort Worth, TX) into one aerial and one underwater speaker. The latter was partially covered with neoprene and oriented away from the cylinder so as to minimize reflected sounds that might have given acoustic information about its contents. The tone signaled the dolphin to swim underwater toward the examination dock (Fig. 1b). During the approach, the dolphin

would briefly view the cylinder with both eyes before resting its chin on a crescent-shaped plastic stirrup 1 m directly beneath it (Fig. 1c). The animal would then rotate its body and with one eye look upward through the contents of the cylinder.

Twenty cylinders were built and used randomly to circumvent the possibility that slight differences in their construction might influence the dolphin's choice. Each cylinder was made of 3-mm-thick clear acrylic plastic measuring 46 cm diameter, and 22 cm high. A 10-cm black band was painted around the middle of the inner and outer surfaces to prevent animals viewing the contents through the cylinder walls. A cylinder was held half-submerged by four wires hung from a frame that rolled along a track extending 40 cm in front of the dock (Fig. 1c). The assembly allowed the trainer to deploy, retrieve, replace, or redeploy any of three prepared cylinders in less than 2 min.

With the dolphin on station, the examiner presented a 400-Hz tone. If the cylinder contained a substance (S+), the animal was required to leave the stirrup within 5 s (timed with a stopwatch) to press a wooden paddle, triggering a spring-actuated flag in the examination dock (Fig. 1c). If the cylinder contained only seawater (S−), the dolphin was required to remain on station for a full 5 s.

If the response was correct, the examiner used a whistle transmitted in air and underwater, signaling the animal to return to the resting dock for a reward of two fish. If incorrect, the examiner would broadcast a "chirping" sound recalling the dolphin to the resting dock without reward. This signal was also used to recall the dolphin during any breakdown in the testing sequence.

Toward the end of the visual discrimination experiment, we initiated a short series of similar trials during which the male dolphin was required to perform the same tasks while blindfolded. The animal was fitted with latex (A. F. Langguth, Ivanhoe, CA) eyecups, worn for up to 30 min at a time, and removed if the dolphin showed signs of discomfort. To avoid visual cues, the eyecups were removed only after the test cylinders were retrieved into the canal.

Test substances, presentation, and retrieval — Oils used in the study are listed in Table 1. We measured the transmission of light through 12 different oils and 22 oil mixtures using a common characteristic, optical density. Light from a 100-W tungsten bulb in a photo-flood reflector (Smith-Victor BD12) covered with a diffusing screen (Smith-Victor D120) was passed through measured thicknesses of oil in a petri dish. Optical density was determined using an Archer 276-116 photo cell (Tandy Corp., Ft. Worth, TX) and a 427-A ohmmeter (Hewlett Packard Inc., Palo Alto, CA), and calibrated using No. 1523422 celluloid filters (Kodak Corp., Rochester, NY). Coefficient of variation of optical densities on 12 individually prepared oil samples measured up to 10 times each was less than 1%.

Each session consisted of blocks of 10 trials, conducted once or twice daily. A trial used one of three cylinders containing either seawater (S−), the principal test substance (S+), or sometimes a novel test substance (probe). Prior to each session, the test substances, the cylinder numbers, and their order of presentation were selected using a computer (Apple Inc., Cupertino, CA) randomization function, modified into a Gellerman (1933) series, without more than three consecutive presentations of either S+ or S− samples. Generally, one test substance was used in a session, with an attempt to equalize the number of S+ and S− presentations. Of the 1733 training and 2133 test presentations, 52% were S+, and 48% were S−.

An animal was tested with a given oil until its performance on both S+ and S− trials was 90% correct or better. Novel oil was introduced outright, or by interjecting it (probe-trials), once or twice within any series of 10 trials with a principal test substance of known detectability (>90% correct performance). If the animal detected the oil, we made this the principal test substance in the next session. If it failed, we reverted to trials with known detectable substances, to assure ourselves that the animal had not lost the behavior but that its failure to respond reflected the limits of detectability. We arbitrarily accepted 75% correct performance as an indication that the animals could detect a substance. This was based on a review of conventionally accepted criteria for discriminatory trials (Nachtigall 1980).

At the conclusion of a series of trials, oil was retrieved in a way that would not contaminate the water. The ends of each cylinder were capped with plywood disks fitted with gaskets (Geocel Corp., Elkhart, IN), and the assembly with its contents was sandwiched tightly together with a bolt running through the middle of the disks (Fig. 1d).

Results — Both dolphins acquired the desired behavior within 6 mo of training, including a 4-mo period needed to change and refine the protocols. The male trained more easily, performed more reliably, and therefore was tested more than the female. Performance on the visual detection trials for both dolphins is shown on Table 2. The female reliably detected 6-mm-thick slicks of crude oil and three refined motor oils, and diesel oil thicker than 25−31 mm (OD > 0.12). To quantify her limits of detection, we tested her using 6-mm-thick slicks of blue-tinted Evinrude 2-cycle motor oil mixed with diesel oil. She could less easily detect oil mixtures than the much thicker diesel slicks of comparable optical density.

The male detected 6-mm slicks of three crude oils, two residual oils, and three refined motor oils (Table 2), all of which had an optical density greater than 0.26. Initially, he did not detect the same thickness of gasoline or diesel fuel (OD ≤ 0.05). He could, however, detect a diesel slick of 17 mm or thicker (OD ≥ 0.08). As did the female, the male detected diesel more reliably (100%) than mixed oil (83%) with the same optical density.

We interrupted visual testing of the male to conduct studies using eyecups. When visual testing resumed after 3 mo, the male's performance improved and his threshold estimates were lower than those obtained in the initial trials (Table 3). He reliably detected diesel slicks as thin as 3 mm (OD < 0.05), and oil mixtures down to an OD of 0.07. Previously he had been unable to detect 6-mm-thick samples of gasoline (OD < 0.05) on only four trials (Table 2); this was not pursued at the time, so as not to extinguish the behavior. After the eyecup experiment, he was retested with the same substance and his performance rose to 74%, close to the

TABLE 2. Performance of two dolphins in detecting crude and refined oils.

Sample[a]	OD[b]	Male		Female	
		No. of trials	% correct	No. of trials	% correct
Crude oil					
Inter-Provincial	>3.0	63	98	—	—
West Texas	>3.0	38	100	—	—
Unidentified	>3.0	29	93	30	97
Residual oil					
Bunker C	>3.0	30	100	—	—
Beach tar	>3.0	30	97	—	—
Refined motor oils					
Quaker SAE 30	0.26	155	98	32	100
Kendall SAE 20	0.26	16	100	30	93
Evinrude 2-cycle	0.79	77	100	54	93
Refined fuel					
Diesel A 35 mm	0.20	30	100	15	100
31 mm	0.16	—	—	28	96
25 mm	0.12	21	95	16	63
17 mm	0.08	23	100	—	—
6 mm	0.05	11	27	—	—
Leaded gasoline	<0.05	4	0	—	—
Mixed oils					
Evinrude:Diesel A					
47:53	0.64	30	100	32	100
25:75	0.50	32	100	32	100
15:85	0.34	32	100	52	96
6:94	0.20	52	100	42	71
3:97	0.12	32	91	—	—
1:99	0.08	18	83	—	—

[a]All samples were 6 mm thick, unless otherwise noted.
[b]Optical density.

established criterion for detection. On retesting, he was still unable to detect the virtually transparent mineral oil.

We determined the male's ability to detect oils while wearing eyecups, by shaping the behavior initially using a styrofoam disk that occupied the entire surface with the cylinder, and gradually changing to oil in the same manner as was done in the visual trials. When first presented with test substances, he detected 12-mm-thick films of Inter-Provincial crude oil (87%), and unidentified crude oil (81%) (Table 4). His performance in detecting Bunker C oil and mineral oil improved slightly when these were churned and contained air bubbles. The dolphin was unable to detect 12-mm-thick samples of West Texas crude oil (56%), or diesel fuel (64%). We then tested him with 6-mm samples of Inter-Provincial crude oil, unidentified crude oil, and diesel fuel (23 trials; 43% correct). He could not detect them. We terminated testing of 6-mm-thick samples to preserve the behavior.

Discussion — Bottlenose dolphins in this study visually discriminated between oil and the uncontaminated surface of the water. The darker the substance, the easier it was to detect. From our observations, we estimate that a naive dolphin can detect oil having an optical density greater than 0.20–0.34. We could not determine the precise thickness of crude oil having this optical density, as the thinnest film of crude oil we could test in our experiments was 1 mm thick. All three crude oil samples of this thickness had optical densities of greater than 3.0, certainly well within the range of perception by the dolphins in this study.

We conclude that dolphins can see the thicker formations of oil that typically occur at the source of a spill (Jordan and Payne 1980), and weathered fractions which form "pancakes" of much thicker viscous oils (Murray 1982). Lighter fractions that disperse into thin sheens (2–30 μm), which comprise most of the spill area (Hollinger and Mennella 1973, National Academy of Sciences 1975) would not be detected easily, if at all, nor would lightly colored refined products such as gasoline, diesel fuel, and solvents that tend to disperse into thin films very rapidly (Jordan and Payne 1980).

The behavior of the male, whose performance improved after repeated testing with light oils, suggests that the threshold optical densities we obtained are not absolute, and that a dolphin's ability to detect the more transparent substances may, in part, depend on prior exposure. Color may be involved as well. On first exposure, blue-tinted oil mixtures were less detectable than amber-colored diesel fuel of the

TABLE 3. Performance of the male dolphin in trials to determine visual detection, after repeated testing at threshold.

Sample[a]	OD[b]	Trials: No. of trials	Trials: % correct
Diesel B 12 mm	0.09	14	100
6 mm	0.06	132	94
4.5 mm	<0.05	30	100
3.0 mm	<0.05	17	94
1.5 mm	<0.05	33	76
0.6 mm	<0.05	4	0
Leaded gasoline	<0.05	47	74
Evinrude:Mineral oil			
10:90	0.20	26	96
6:94	0.12	93	88
5:95	0.09	30	83
4:96	0.07	29	79
3:97	0.06	3	0
Evinrude:Diesel B			
1:99	0.08	42	98
Mineral oil (12 mm)	<0.05	17	18

[a]All samples were 6 mm thick, unless otherwise noted.
[b]Optical density.

TABLE 4. Performance of the male dolphin, while blindfolded, in detecting crude and refined oils.[a]

Sample	Trials: No. of trials	Trials: % correct
Inter-Provincial crude	82	87
West Texas crude	16	56
Unidentified crude	60	81
Diesel	22	64
Bunker C (whipped)[b]	30	88
Bunker C	141	68
Mineral (whipped)	18	94
Mineral	64	70
Styrofoam (control)	97	91

[a]All oil samples were 12 mm thick.
[b]Oil and seawater whipped with an egg beater to entrap air bubbles.

same optical density. The optical densities may not have been exactly the same, depending on the spectrum of the light source and the sensitivity of the photocell; these were not determined. Nevertheless, the difference in thresholds for detecting the amber and blue-tinted substances was far less pronounced after learning. Though dolphins have little or no color vision, they appear to have greater sensitivity to light in the blue-green portion of the spectrum (Madsen and Herman 1980). Therefore, we expected them to see the oil mixtures more readily. Their inability to do so may have been due to lack of contrast when viewing the light blue sample against the sky.

When vision is impaired by low light or turbid water, it might be possible for dolphins, as it was for the male in our study, to use other senses to detect thicker, high-viscosity substances or oils churned by wind and wave action. It will be important to determine how available light and other features of the environment influence a dolphin's ability to detect oil.

Acknowledgments — We thank A. Rodriguez, C. Garrigan, D. Matthews, C. Smith, and L. Valladeres of IDR for dolphin training, handling, and testing; and V. Lounsbury, C. Robinson, and G. Van Drunen (Guelph) for technical assistance and graphics. Bambino Inc., Los Angeles, CA generously donated the tone generators. J. Rodriguez, managing director of IDR, provided facilities and administrative support. We thank W. Evans, Hubbs-Sea World, San Diego, CA; T. G. Smith, Arctic Biol. Station, Ste. Anne de Bellevue, Que.; E. Bailey, University of Guelph; and especially P. Nachtigall, Naval Ocean Systems Center, HI, for advice and critical review of the manuscript. This study was funded by a contract from the U.S. Department of the Interior, Minerals Management Service (No. AA551-CT9-29).

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Reaction of Bottlenose Dolphins, *Tursiops truncatus*, to a Controlled Oil Spill

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SMITH, T. G., J. R. GERACI, AND D. J. ST. AUBIN. 1983. Reaction of bottlenose dolphins, *Tursiops truncatus*, to a controlled oil spill. Can. J. Fish. Aquat. Sci. 40: 1522–1525.

Three captive bottlenose dolphins, *Tursiops truncatus*, were observed in an ocean pen measuring 14 × 11 m, divided into three equal areas by oil-containment booms. Each dolphin was placed in the pen alone for 4 d with no oil present, and 2 d with dark-colored mineral oil in one of the areas. We noted their area of surfacing, underwater movements, dive times, and reactions. After a few brief contacts with the oil, dolphins completely avoided surfacing in the slick. The oil also acted as a temporary barrier restricting their underwater movement.

SMITH, T. G., J. R. GERACI, AND D. J. ST. AUBIN. 1983. Reaction of bottlenose dolphins, *Tursiops truncatus*, to a controlled oil spill. Can. J. Fish. Aquat. Sci. 40: 1522–1525.

Nous avons étudié deux dauphins à gros nez, *Tursiops truncatus*, dans un enclos mesurant 11 m × 14 m. Ce bassin marin était divisé en trois parties égales par des jupes de rétention. Chaque dauphin a été placé seul dans l'enclos pendant quatre jours sans qu'il y ait d'huile et ensuite pour une période de deux jours alors qu'il y avait de l'huile minérale colorée dans une des sections. Nous avons noté l'endroit où les dauphins respiraient, leurs mouvements sous l'eau, la longueur de plongée et leur comportement en général. Après quelques brefs contacts avec l'huile, les dauphins évitaient complètement de franchir la couche d'huile pour respirer. La section huilée constituait aussi une barrière temporaire qui restreignait le mouvement sous-marin.

Received January 11, 1983
Accepted May 31, 1983

Reçu le 11 janvier 1983
Accepté le 31 mai 1983

UNDER experimental conditions, bottlenose dolphins, *Tursiops truncatus*, can detect varying grades of crude and refined oils on the surface of the water (Geraci et al. 1983). Their reaction to these substances at sea has not been established, but both odontocetes and mysticetes have been seen feeding in the midst of oil slicks (Goodale et al. 1981; Gruber 1981). Either they did not detect the oil, were indifferent to its presence, or chose not to avoid it, perhaps because of some overriding (feeding) motivation.

Our objective was to determine whether captive bottlenose dolphins, under controlled conditions, would avoid a detectable slick of colored, nontoxic mineral oil. We did this by confining the animals to a pen subdivided into three areas. After establishing their patterns of behavior, we added oil to one of the areas, and determined the reaction of each dolphin.

Printed in Canada (J7198)
Imprimé au Canada (J7198)

Materials and methods — Three female dolphins, designated A, B, and C, aged ~4 yr were captured in the Gulf of Mexico near Biloxi, MS, in July 1980 and transported to the Institute for Delphinid Research, Grassy Key, FL. They were kept together in seawater pens, and fed a daily ration of herring to provide 60–70 kcal·kg^{-1} body weight (0.25–0.29 J·kg^{-1} body weight). The dolphins were not trained to perform any other tasks. They were handled periodically for skin studies over a 9-mo period prior to this experiment. The animals were in good health as judged by routine clinical examination, feeding behavior, and blood studies.

The study area was a rectangular pen 14 × 11 m (154 m^2) formed by a chain-link fence on three sides and on the fourth by a solid filled causeway. The pool was subdivided into three rectangles using booms (Oil Containment Systems Corp., Cocoa, FL) with floats projecting 15 cm above the surface and weighted skirts submerged to 30 cm. Each of the three rectangles formed by the booms measured 4.5 × 11 m (50 m^2)

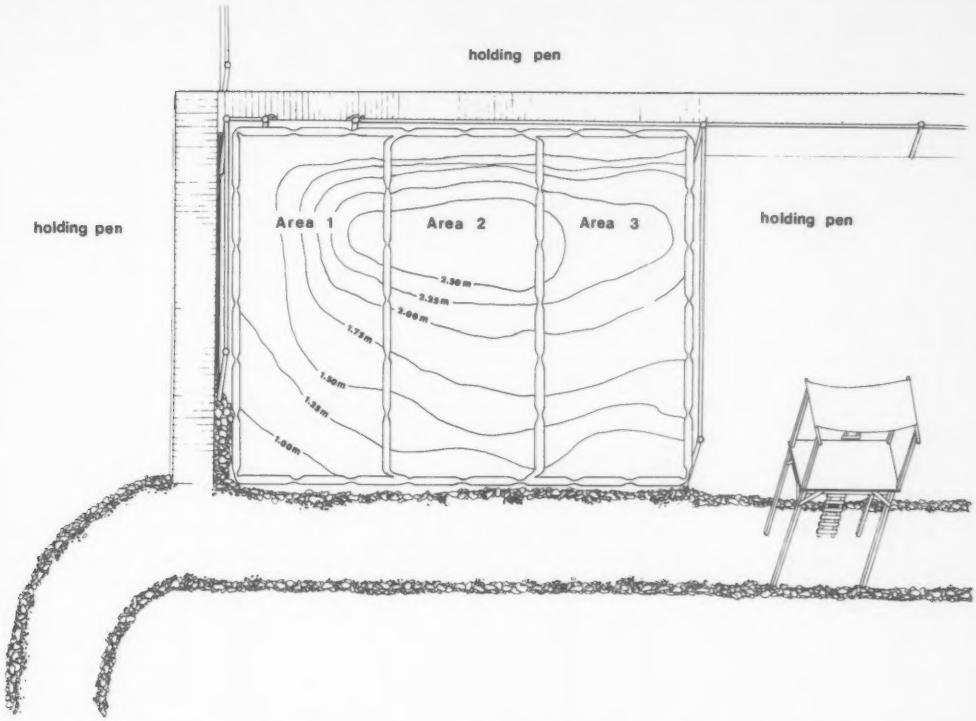

FIG. 1. Test pool used in oil-avoidance study, showing depth contours (at mean high tide), position of oil-confining booms, relationship to adjacent dolphin-holding pens, and location of observation tower. After a series of control sessions, colored mineral oil was added to Area 2.

(Fig. 1). The dolphins entered the pen through a wire-mesh gate into area 1. During the experiment, the dolphins were able to interact visually and acoustically with dolphins in adjacent holding pens.

A 5-m-high observation tower was erected on the causeway 3 m from the north corner of the test pool. During the observation periods, video recordings were made from the tower using a Hitachi GP-5U camera coupled to a Quasar VH5160SW recorder. Verbal accounts were simultaneously recorded using a Uher 4200 stereophonic tape recorder, and a Sony BM 10 cassette recorder.

The animals were acclimated to the oil booms by placing a free-floating section of boom in their holding pen for a period of 2 wk. The three animals together were then introduced daily for 4 d to the study area which contained several booms in various configurations. For 4 d thereafter, each dolphin was introduced alone for up to 4 $h \cdot d^{-1}$. During this time, the final boom configuration (Fig. 1) was established.

Following the acclimation period, we ran a series of control (oil-free) sessions, in which each animal was put into the pen alone for 7–9 h on four nonconsecutive days. Observations were made as soon as the animal entered the pen, and at 2-h intervals thereafter. Each of the four daily periods included 30 min to note the location of each surfacing, and 15 min during which surfacings, underwater movements, dive duration, and behavioral traits of the animal were recorded.

We determined frequency of occupation by noting the underwater movement of each animal. After a dolphin would submerge, we counted each new area it entered as a single occupation. We did not count the area in which it dove, unless it resurfaced there. For this calculation, we did not consider the total time during which an animal occupied a given area.

After the control sessions, 416 L of oil was added to area 2 resulting in a surface slick 1 cm thick. The basis for selecting area 2 is developed fully under Results. Each dolphin was then placed in the study area on two nonconsecutive days, and its behavior recorded as described for the control sessions.

We used Primol 355 (Exxon Company, Houston, TX 77001), an odorless, tasteless, nontoxic, highly refined mineral oil with a viscosity (67.8 centistokes at 40°C, Exxon Data Sheet DG-2H) matching that which we have determined for weathered medium-weight crude oils. Artist's oil paint colorant (Liquitex Series 1147, No. 244 Ivory Black, Binney & Smith, Easton, PA 18042) containing bone black, aluminum stearate, and linseed oil, was added to the Primol at a

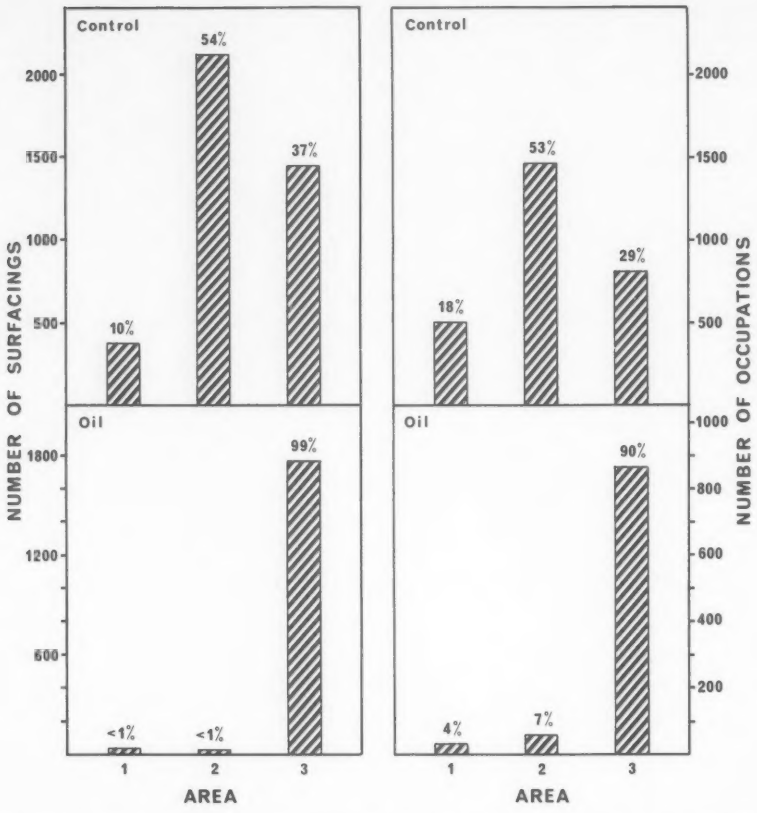

FIG. 2. Summary of surfacings and underwater occupations of the three pool areas by three dolphins during the oil-free and oiled sessions.

concentration of 0.5 $g \cdot L^{-1}$, to simulate the dark color of crude oil. A 1-cm-thick layer of the colored oil had an optical density of 0.7, which Geraci et al. (1983) determined to be well within the range of detectability for bottlenose dolphins. By the third test (oil) session, the colorant had separated to some extent, forming dark aggregations. Uniform optical properties were reestablished by adding 100 L of mineral oil containing 1.0 $g \cdot L^{-1}$ of colorant. Any luminescent sheen noted in areas 1 and 3 was removed by absorbent pads (Sorbent type 126 and 156; 3M Corp., St. Paul, MN 55144) at the beginning of each test session. These pads were also used to clean up all of the oil at the end of the experiment.

We treated the data using a Friedman two-way analysis of variance by ranks (Siegel 1956). Surfacing and occupation frequencies for each area were examined separately for the 16 control and 8 experimental observation periods. We analyzed for chronological and individual animal trends, then grouped the data by observation period to determine daily patterns. Mean diving times were compared using Student's *t*-test.

Results — The dolphins behaved normally throughout the acclimation period, though their interactions were more conservative than when they were in their holding pen. When alone in the study area, they swam slowly and surfaced regularly to breathe. There was little reaction to the booms, except by dolphin B which nudged and occasionally dunked it with her snout. The presence of dolphins in adjacent holding pens did not obviously affect the test animal's behavior.

Throughout the acclimation period, all three dolphins showed a preference for the portion of the pool with the deepest water (>1.75 m) (Fig. 1). With the booms in their final configuration, this represented test areas 2 and 3. This preference persisted during the oil-free sessions and was statistically significant ($\chi^2 > 17.28$, df = 2, $P < 0.001$ in all cases), with no significant difference among the animals.

No change was seen within each day in the frequency of surfacing, or duration of dives for any of the dolphins. However, an increase in underwater movement was seen in dolphin B ($\chi^2 = 25.58$, df = 15, $P < 0.05$) during the control

sessions. During the entire control period, more than 90% of the 3924 surfacings, and over 80% of the 2789 observed occupations occurred in areas 2 and 3. We therefore chose to place the oil in one of these areas, and arbitrarily selected test area 2.

In this experimental setting, dolphins B, C, and A initially avoided the oiled areas for 5, 35, and 53 min, respectively. Within 2 h of the 1st day, all three came into contact with the oil from 2 to 7 times for a total of 12 contacts. On three occasions, after touching the oil with the dorsal fin, the animals appeared to startle, and swam rapidly into area 3. Eight other times they surfaced through the oil without breathing, submerged abruptly, then moved quickly out from under the oil. On two such occasions, the dolphins returned to area 3, where they blew clouds of bubbles, one slapped its tail on the surface, the other exhaled explosively.

On their second exposure, 4 d later, none of the dolphins contacted the oil. One dolphin showed a significant change in movements, somewhat increasing her underwater use of the oiled area ($\chi^2 = 16.72$, df = 7, $P < 0.05$). Number of surfacings and occupations for all three dolphins were grouped for the control and test sessions (Fig. 2). This illustrates their almost complete avoidance of areas 1 and 2 when oil was present.

There was no difference in the mean dive times of individual dolphins throughout the observation periods. This was true for both control and test sessions.

Discussion — The dolphins in this study avoided oil. They clearly could detect it, as they swam under the oil, surfaced alongside in the clean water, but avoided contacting the oil itself. Their initial reluctance to contact it may have been their natural response to any new stimulus, and does not necessarily imply a conscious avoidance of oil per se. Within an hour after sighting the oil, each dolphin emerged in it, either accidentally or as part of an investigative process. In every case, the dolphins reacted immediately and overtly with a startle response followed by behavior which we usually associate with stress or annoyance. Yet the oil was innocuous, indicating that another physical property of the oil, viscosity perhaps, was enough to disturb the animals. The behavior suggests that the tactile sense may play an important role in a dolphin's reaction to oil.

All contacts with oil occurred during the first 2 h of exposure; the dolphins did not again surface in the oil either that day or when reintroduced to the pen 4 d later. In fact, their aversion to oil prevented all three dolphins from swimming beneath it to area 1; the oil slick acted as a barrier impeding their movement. This might be expected to have some consequence in situations where dolphins, during a spill, become entrapped in bays, rivers, or ice leads, and whose only escape route is blocked by oil. For some individuals, this barrier effect might diminish over time, as suggested by the behavior of one of the dolphins in our study, which increased its movements under the oil and beyond, by the 2nd day of exposure.

These studies have shown that bottlenose dolphins can detect and will avoid oil. This was a response we purposely isolated under experimental conditions, without attempting to address social and environmental factors that might influence free-ranging animals. We are aware of only two records of cetaceans remaining in the proximity of oil spills, in both instances, without apparent reaction or consequences (Goodale et al. 1981; Gruber 1981). Their ability to detect the oil under oceanic conditions may not have been as keen as that shown for captive animals (Geraci et al. 1983). On the other hand, the animals' dependence on the area for food and social interaction may have influenced what we have found to be a basic avoidance reaction.

Acknowledgements — We thank G. Van Drunen and C. Robinson (University of Guelph), E. Gardner and the training staff of the Institute for Delphinid Research (IDR), and G. Sleno (Arctic Biological Station) for technical assistance; and Dr M. Fanouss, MacDonald College, Ste. Anne de Bellevue, Que., for statistical advice. We especially thank J. Rodriguez, managing director of IDR for providing facilities and administrative support. This study was funded by a contract from the U.S. Dep. of the Interior, Minerals Management Service (No. AA551-CT9-29).

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Feasibility of Snow Clearing to Improve Dissolved Oxygen Conditions in a Winterkill Lake

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Although periodic mechanical snow removal from the surface of an experimental plot on Rock Lake, southern Manitoba, between January and February, did not provide an expected increase of dissolved oxygen levels that would reduce the likelihood of fish winterkill in the localized area of the lake, it provided a basis for analyzing the practicality and feasibility of the method. The minimum lake area to be kept clear of snow for prevention of winterkill was calculated to be 15% of the total lake area. Snow clearing should start soon after freeze-up to provide at least 0.3 $g \cdot m^{-2} \cdot d^{-1}$ dissolved oxygen needed to compensate for bacterial oxygen uptake during the winter months.

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Le présent rapport porte sur l'enlèvement mécanique de la neige, en janvier et février, de la surface d'une partie expérimentale du lac Rock, dans le sud du Manitoba. Même si le procédé n'a pas entraîné l'augmentation attendue des niveaux d'oxygène dissous qui réduirait la probabilité de mortalité excessive des poissons en hiver dans cette partie du lac, il a fourni une base pour l'analyse de l'applicabilité et de la faisabilité de la méthode. Selon les calculs, la superficie minimale du lac à déneiger pour prévenir une mortalité excessive s'élève à 15 % de la superficie totale. Le déneigement devrait commencer dès le gel du lac afin de fournir au moins 0,3 $g \cdot m^{-2} \cdot j^{-1}$ d'oxygène dissous nécessaire pour compenser la captation bactérienne d'oxygène pendant l'hiver.

Received February 18, 1983
Accepted May 31, 1983

Reçu le 18 février 1983
Accepté le 31 mai 1983

ANOXIC conditions and reduced water quality are a frequent phenomenon in many shallow eutrophic lakes in central North America and northern Europe that are subjected to long periods of ice and snow cover. When fish are present, winterkill develops as dissolved oxygen declines to critical levels. Oxygen depletion is caused by bacterial decomposition of organic matter at a time when excessive ice and snow prevents oxygen input through primary production and surface aeration. This phenomenon has been described by various authors (Greenbank 1945; Scidmore 1957; Nickum 1970). More recently, Lasenby (1975) and Mathias and Barica (1980) ana'yzed limnological factors controlling oxygen depletion in ice-covered lakes (summer Secchi depth or sediment are lake volume ratio, respectively). Barica and Mathias (1979) related oxygen-uptake rates to lake morphometry and developed a predictive model for determining critical time for a lake to reach total anoxia. Jackson and Lasenby (1982) presented a method for predicting oxygen profiles under ice cover.

The prevention of periodic winterkill has led to a number of trial methods designed to maintain or improve under-ice dissolved oxygen levels. Wirth (1970) reviewed some of these procedures and described the use of a type of aeration system in use in some Wisconsin lakes. Most aeration systems used in the past have been undersized (Pastorok et al. 1981) and to aerate artificially large lakes at recommended rates was often cost prohibitive. This was confirmed on Rock Lake

Printed in Canada (J7256)
Imprimé au Canada (J7256)

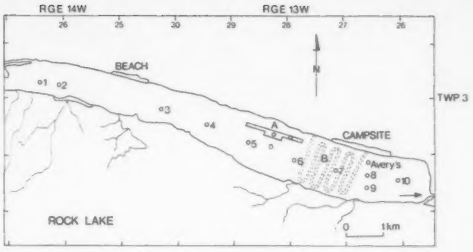

FIG. 1. Rock Lake with the sampling sites (numbered). (A) Experimental clearing plot; (B), originally considered snow clearing pattern for whole lake restoration.

and a neighboring lake, Pelican Lake, when localized aeration between 1974 and 1976 could not prevent fish kills (W. Howard unpublished data).

Snow removal from an ice surface has often been suggested as a natural means of increasing oxygen levels through increased light penetration that boosts primary production. Müller (1957) tried this method experimentally on three small lakes in northern Germany using 0.1-ha snow-free "windows." Quite positive results were noted in the cleared area. Paulin (1960) reported on a successful aversion of winterkill in a Wisconsin lake by snow plowing.

In this report, we present the results of a snow-clearing experiment on Rock Lake, southern Manitoba, that was conducted in an effort to save fish stocks and to test the feasibility of this method on larger lakes and a larger snow-free area.

Study area — Rock Lake is situated along the Pembina River Valley southwest of Winnipeg, Man. (Fig. 1). The lake has a surface area of about 1720 ha, a length approaching 13 km, and a mean width of ~1 km. It is very shallow with a maximum depth of 3.8 m and a mean depth less than 3.0 m.

The drainage area contributing to Rock Lake is ~4600 km^2 and inflows have ranged from zero to an estimated daily maximum in excess of 330 m^3/s. Seasonal flows from several north-shore springs add a further unmeasured flow to the lake. The flushing rate of Rock Lake has been estimated at 2.8 volume$\cdot y^{-1}$ (Anon. 1976).

Rock Lake is hypereutrophic and develops heavy *Aphanizomenon flos-aquae* and *Microcystis* sp. blooms in July–August that reach maximum levels of 292 μg/L chlorophyll *a* (R. J. Allan, NWRI, Burlington, unpublished data). Phosphorus loading to Rock Lake have been estimated at 1.3 $g\cdot m^{-2}\cdot yr^{-1}$ (Anon. 1976).

Excessive Rock Lake primary production and the subsequent decomposition of organic materials have produced periods of degraded water quality. Under ice cover which usually ranges from early November to early April, some degree of fish winterkill can be expected on the average in about 50% of the winters. In summer, algae accumulations detract from most forms of water-based recreation and periodically, fish summerkills have been reported.

Existing recreational facilities include beaches, picnic areas, campgrounds, and church camps. Cottaging, boating, and angling are popular forms of recreation. Depending on the severity and frequency of fish kills, summer and winter angling for northern pike (*Esox lucius*), walleye (*Stizostedion vitreum vitreum*), and yellow perch (*Perca flavescens*) has been intense in some years.

Methods — Limited yearly dissolved oxygen data for Rock Lake were available for historical background and comparison. Regular, more extensive, winter monitoring began in 1979/80 and continued through the winter of 1981/82. Sample data included ice thickness, snow depth, light readings, dissolved oxygen, soluble reactive phosphorus, pH, ammonium nitrogen, chlorophyll *a*, and conductivity. *The Chemical Analysis of Freshwater* (Stainton et al. 1974) was followed for nutrient analyses. Dissolved oxygen (DO) was measured at 1-m depth intervals. During critical sampling periods a Materflex sampling pump was used to sample more accurately levels of the water column.

Light readings were taken at the ice surface and at various depth intervals with a Lambda LI-1925 underwater sensor and a LI-185 meter. Use of a collapsible arm that fits through an 8-in.- (1 in. = 25.4 mm) diameter auger hole (J. Gibson unpublished method) allowed under-ice light monitorings. Photon values were measured directly in $\mu Einst\cdot m^{-2}\cdot s^{-1}$ and a conversion factor of 1.4 was applied to all readings to allow cross comparison in both air and water (Shearer 1976).

In 1981/82, sampling began on Rock Lake on December 22, 1981 and continued through to March 17, 1982. Once snow clearing began, sampling was repeated every 2 wk. The lake was regularly sampled at three sites: the cleared area, uncleared control areas, and at a location near the end of the lake (Avery's, Fig. 1). Two uncleared sites about 300 m away from the cleared strip were used as a control.

Snow clearing was accomplished with a rubber-tired tractor and a rear-mounted power-take-off driven rotary snowblower 2.4 m in width. Clearing began January 13, 1982, when dissolved oxygen concentrations had declined to about 5 mg/L. Snow depths had reached 20 cm in many areas and initial clearing of the hard-packed snow progressed much slower than expected. A rectangular area of about 75 × 1500 m (11.2 ha) had been designated for clearing, but because of limited financial resources and the slow snow clearing rate, the area was reduced to 50 × 1500 m. Later, the central portion of the strip was enlarged by a further 200 × 300 m in an effort to relate cleared area configuration to possible variations in dissolved oxygen production and snow clearing frequency requirements (total 12 ha). It was anticipated that if proven successful, the snow clearing area would be extended to cover about one third of the lake in a strip-like pattern (Fig. 1, B).

Between January 13 and 24, 1982, 50 h of snowblowing was required to clear this 12-ha zone. The prevailing winds kept most of the central block clear of snow but on March 10 and 11, 1982, a further 11 h of snow blowing was required to clear fringe areas. The total cost of snow clearing totalled $1952 (61 h at $32.00/h or ~$165.00 per hectare).

Results — Figure 2 shows the variability in dissolved oxygen, soluble reactive phosphorus, ammonium nitrogen, and chlorophyll *a* at one of the monitoring sites (Avery's) from 1979/80 to 1981/82. Other stations showed similar

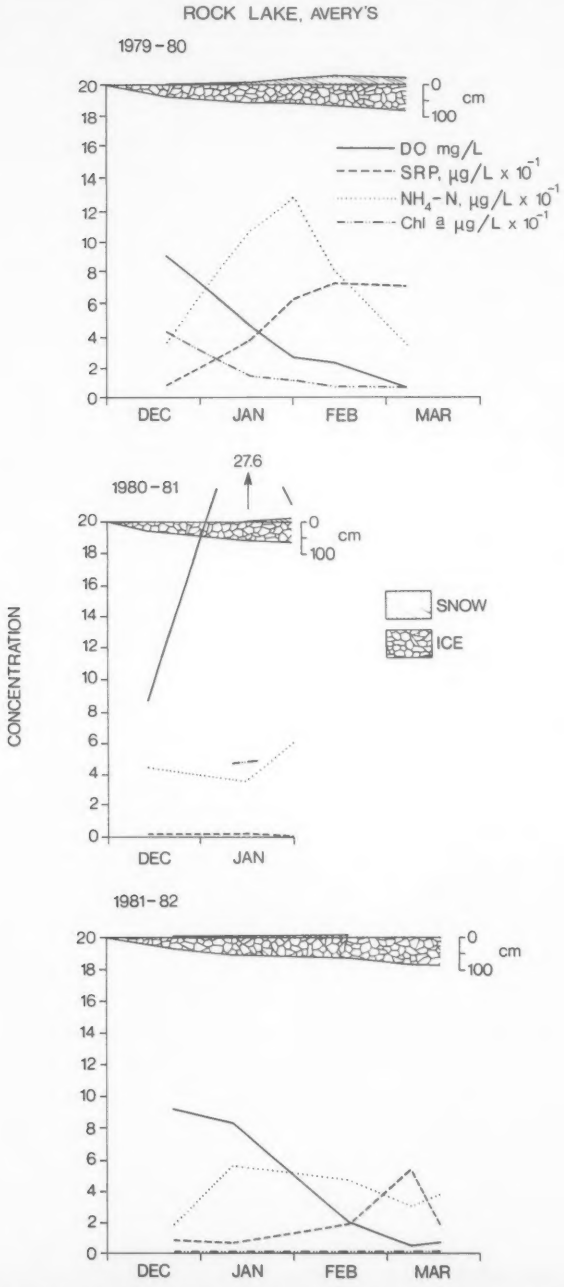

FIG. 2. Dissolved oxygen (DO), soluble reactive phosphorus (SRP), ammonia-N, and chlorophyll *a* in Rock Lake at Avery's sampling stations 8 and 9 (mean values for three sites, 0–2 m).

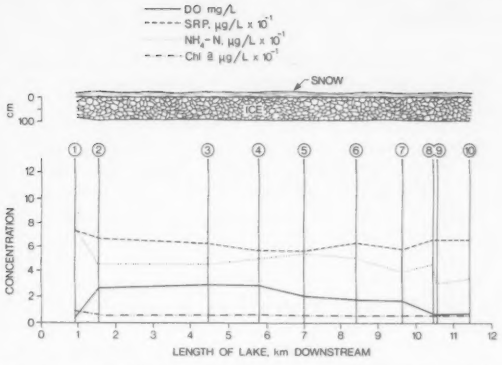

FIG. 3. A longitudinal profile of dissolved oxygen (DO), soluble reactive phosphorus (SRP), ammonia-N, and chlorophyll *a* in Rock Lake on March 6, 1982 (peak of the winterkill).

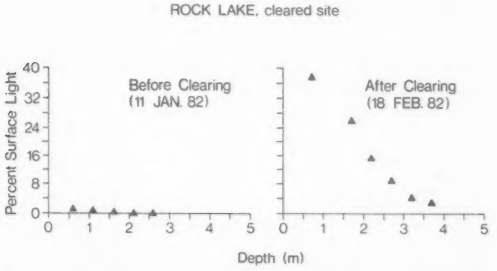

FIG. 4. Characteristic light readings before and after snow clearing at cleared site in Rock Lake. Values are percent of surface reading.

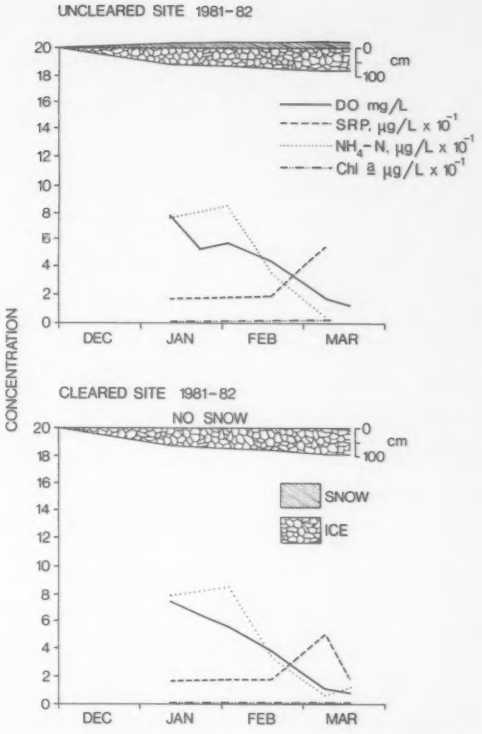

FIG. 5. Mean dissolved oxygen (DO), soluble reactive phosphorus (SRP), ammonia-N, and chlorophyll *a* concentrations at the uncleared and cleared site (0–2 m).

results. True winterkill conditions developed in 1979/80 and 1981/82 when dissolved oxygen levels dropped to about 1.0 mg/L or less. No winterkill developed in 1980/81; almost no snow cover allowed algal bloom development and dissolved oxygen levels reached about 300% supersaturation. Sampling was discontinued in 1980/81 because of the lack of snow and a minimum winterkill hazard.

There have always been considerable differences in areal distribution of DO concentrations each year over the longitudinal profile of Rock Lake. Figure 3 shows DO values and other selected water quality characteristics in March 6, 1982, at the peak of the winterkill. The minimum DO levels (0.5–0.7) can be considered as normal lake values suggested by the winterkill prediction model (Barica and Mathias 1979), whereas the levels of 1.7–2.7 are likely affected by the addition of oxygenated water from the south tributaries and springs, and the overall west–east decrease in the lake's depths and a slight increase in snow cover due to the prevailing winds.

There was a positive relationship between snow clearing and light transfer through the ice (Fig. 4). Two other stations showed similar results.

Although light measurements showed a straightforward effect of snow clearing operations, the DO and nutrient–chlorophyll data did not (Fig. 5). The differences between the two groups were statistically insignificant, and DO levels in the uncleared area were even slightly higher than in the cleared area. This discrepancy may have been caused by the natural areal variability of the DO levels over the whole lake. It, however, did not provide any indication that the DO levels in the cleared area were significantly better than in the adjacent uncleared area.

Algal biomass (as chlorophyll *a*) was minimal in all areas. However, phytoplankton composition showed a significant difference between the cleared area and the Avery's site downstream (uncleared). Avery's area showed about one third less biomass than the cleared area. *Chromulina* sp., *Chlamydomonas* sp. (8–12 µm), *Cryptomonas erosa*, *Synechococcus* sp., *Pseudoanabaena* sp., and *Monoraphidium contortum* were predominant at Avery's. Larger *Chlamydomonas* sp. (15–20 µm), *Rhodomonas lacustris*, *Chromulina* sp., and *Monoraphidium contortum* dominated the cleared area (H. Kling, Freshwater Institute, Winnipeg, unpublished data).

Discussion — The results of the snow clearing experiment on Rock Lake were disappointing. Although performed on an area 120 times larger than Müller's (1957) experiment, which was the main rationale of the experiment, it did not provide the same dissolved oxygen improvement. Even though snow clearing produced significant increases in light transfer through the ice, photosynthetic activity did not increase primary production. There was no significant difference between dissolved oxygen levels in the cleared area versus the uncleared areas. In fact, average dissolved oxygen levels in the uncleared area were slightly higher than in the cleared area (0.94 mg/L versus 1.21 mg/L), but higher than at a downstream site at Avery's, some 3 km from the cleared area (0.68 mg/L). The lack of improvement in dissolved oxygen levels in the cleared area was likely impeded by significant water movement under ice. This could be caused by spring activity, normal cyclonic pattern of water movement, convection currents between different water density areas and shifting ice masses. Algal populations and oxygenated conditions may slowly develop in the cleared area but passively drift to uncleared areas before significant growth and reproduction can occur, with immediate reduction of dissolved oxygen levels by immediate sediment oxygen demand which is known to be high in prairie lakes (Barica 1975). Such a hypothesis requires further testing.

We suggest that the size of the cleared area relative to size of the lake is the factor deciding the success of the operation. In the winter of 1980/81, there was very little snow cover and the snow-clear area extended to almost 100% of the lake. In that winter, supersaturated dissolved oxygen levels (about 300%) persisted through January and likely also beyond (sampling discontinued for no winterkill risk). During this period, the aerial oxygen productivity was about $2\ g \cdot m^{-2} \cdot d^{-1}$ (from Fig. 2). In 1981/82, the cleared area on Rock Lake represented only about 0.7% of the lake surface area. A parallel snow clearing experiment on Oak Lake, Manitoba, in 1981/82, produced slightly higher, statistically significant, mean dissolved oxygen levels in the cleared area relative to the uncleared area. Close to 50 ha were cleared on Oak Lake which represents about 1.7% of the lake surface area (W. Howard, Manitoba Department of Natural Resources, unpublished data). However, Paulin (1960) reported favorable results by clearing ~20% of a 195-ha lake.

Mathias and Barica (1980) arrived at a conclusion based on four sets of Canadian lakes (prairie, southeastern Ontario, Arctic, and experimental lakes area of the Freshwater Institute, Winnipeg), showing that oxygen depletion in ice-covered lakes is governed by the lake volume:sediment area ratio. The same analogy can be applied to lake volume:clear (sediment) area ratio, or simply clear area:total sediment area. Thus, in the case of Rock Lake with almost no snow cover in 1980/81 (100% clear area), this ratio was close to 1; for Paulin's lakes (1960), about 0.2 but for Rock and Oak lakes, only 0.007–0.017. At these low ratios, the cleared area was not able to produce sufficient algal biomass and corresponding oxygen levels for the whole lake or its larger parts.

The "negative" results of the Rock Lake experiment, however, provided a valuable insight into the problem. We are now able to recommend some improvements based on better understanding of the process.

Extent and duration of snow clearing — Shallow eutrophic lakes in central North America are known to experience a gradual reduction of their total oxygen mass at a rate between 0.2 and $0.4\ g \cdot m^{-2} \cdot d^{-1}$ DO, between December and March, depending on the mean depth. This corresponds to about $0.3\ g \cdot m^{-2} \cdot d^{-1}$ for the Rock Lake's mean depth of 2.9 m (Barica and Mathias 1979). For a "critical" depletion period of 90 d (Barica and Mathias 1979) this amounts to $0.3 \times 90 = 27\ g \cdot m^{-2} \cdot d^{-1}$ DO. This means that the same amount of dissolved oxygen or more would have to be supplied by primary production during the same period to compensate for oxygen uptake and maintain the minimum required oxygen levels in the water column.

This is nevertheless achievable in the eutrophic prairie lakes which develop heavy algal blooms under the ice in the first, snow-clear half of the winter. Rock Lake shows an example: the December–January rate is about $2\ g \cdot m^{-2} \cdot d^{-1}$ DO (Fig. 2). If this rate is maintained for 90 d, it will result in a gross production $2.0 \times 90 = 180\ g \cdot m^{-2} \cdot d^{-1}$ DO, compared to $27\ g \cdot m^{-2} \cdot d^{-1}$ required for whole lake respiration. Thus, if a 100% snow-clear area can supply $180\ g \cdot m^{-2} \cdot d^{-1}$ DO, required minimum $27\ g \cdot m^{-2} \cdot d^{-1}$ DO will be supplied by $27 \times 100/180 = 15\%$ or 258 ha of the total lake area to provide necessary DO to offset the uptake. This value agrees well with the Paulin successful clearing area of 20%. Based on the operational cost of ~$165.00 per hectare, the total cost for clearing of 15% of the total lake area would represent about $42 500.

It is now obvious that snow clearing has to maintain a snow-free area for the whole critical period between December and early March, to maintain the early winter high productivity. Once the lake starts the decline of DO levels (usually from mid-December on if snow covered), it may be difficult to revive the primary production. This extends substantially the operation period and would increase the cost of snow clearing by ~50%.

Based on Rock Lake results, and the high cost involved, we would hesitate to recommend snow clearing as an economically viable method for large lakes. However, the method is still feasible in small prairie lakes (up to 20 ha) and dugouts for overwintering the fish stocks, mainly for extensive aquaculture of rainbow trout (*Salmo gairdneri*) (Lawler et al. 1974). For large recreational lakes, conventional measures (reduction in nutrient loading, in-lake nutrient inactivation, etc.) may be more effective in the long run. An increase in the mean depth (Barica and Mathias 1979) would increase winter oxygen storage capacity to offset the uptake. These alternatives present other social and economic difficulties but would reduce winterkill probability permanently.

Acknowledgments — We are indebted to Jack Mathias for his valuable input and suggestions for the revised version and to Maurice Roy and John Tisdale for field and laboratory assistance.

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Comment on Meristic Variation in Beaked Redfishes, *Sebastes mentella* and *S. fasciatus*, in the Northwest Atlantic

COMMENT

Following the recent separation of *Sebastes fasciatus* and *S. mentella* (Robins et al. 1980), there is an urgent need for a reconsideration of all aspects of the biology of these fishes, to determine the characteristics of each and the differences between them. One of the first necessities is a thorough knowledge of their distributions based on detailed surveys and accurate identifications. When planning these surveys, Ni's (1982) recent summary of historical meristic data will undoubtedly prove useful, as its preliminary versions (Ni 1981a, b) have already proved.

However, three of Ni's points need further consideration. The first of these concerns Ni's (1982) suggestions of vernacular names for *S. fasciatus*. He correctly rejects the "Labrador redfish" used by Robins et al. (1980), but then suggests the use of "rosefish," "bank redfish," *and* "shelf redfish" (the latter ascribed to me, though it was originally proposed by Dr J. McGlade, Marine Fish Division, Bedford Institute of Oceanography). For at least the third of these names, Ni has drawn on an extensive private correspondence between himself, Dr Robins, Dr W. M. Eschmeyer, and myself. In the course of that correspondence, these three names, and several others, were proposed, and the objections to each fully considered. A final decision of the Committee on Names of Fishes is still awaited, but in the meanwhile, Ni can only further confuse an already complex situation by publicly proposing multiple alternatives.

More importantly, his study is based on an assumption of negligible intraspecific geographic variation in vertebral and anal fin ray frequencies. He suggests four pieces of evidence in support of this assumption: constancy of frequencies between areas in previous studies, the pattern of temporal variation in vertebral frequency, the absence of significant differences in frequencies between depth zones if certain zones are eliminated, and the distinct clusters of NAFO Division/depth zones in his data. Unfortunately, most of these data were extracted from studies by Barsukov (1972) and Barsukov and Zakharov (1972). Those authors compared samples of the two species, but did not state how they identified the individuals. Ni (1982) also used Litvinenko's (1974) data, but the latter relied on identifications performed by Barsukov and Zakharov. As anal fin ray count seems to be the best external character for separating these species (Ni 1981c), it is likely that it was involved in their identifications. Vertebral frequency, which Barsukov (1972) presented as the first character distinguishing these species, may also have been used. To support the geographic constancy of a character using groupings based on that character is circular reasoning. Indeed, the only characters known to be able to distinguish individual *S. mentella* and *S. fasciatus* are extrinsic gas-bladder muscle route (Ni 1981d), frequency of subcaudal melanophores in the larvae (which is applicable only to pregnant females; Templeman 1980), and electrophoretic patterns (Dr J. McGlade personal communication). The meristic counts of specimens identified by these characters certainly support intraspecific geographic constancy, but they have all been collected from between Hamilton Bank, Labrador, and Banquereau Bank, Nova Scotia, about half of the latitudinal range considered by Ni (1982).

The other evidence is even less supportive of Ni's (1982) assumption. Within-area comparisons between years or between depths can give no indication of between-area relationships. Meristic characters in these species seem to be correlated (cf. Barsukov and Zakharov 1972) such that seven anal fin rays commonly co-occur with 29 vertebrae and nine rays with 30 or 31 vertebrae. Given this relationship and three discretely distributed characters, each of which can take at most only eight values, it is hardly surprising that a cluster analysis should group areas with a predominance of low counts separately from areas with predominantly high ones (not to mention the 14 out of 71 zones which did not fit either cluster, by Ni's (1982) own designation of "mixture"). Such clusters are simply not relevant to an examination of intraspecific variation.

In summary, from my own studies of this genus, I suspect that the intraspecific variation in anal fin ray and vertebral frequencies of *S. fasciatus* and *S. mentella* is much less than even the tiny interspecific difference between them. This would be consistent with Ni's (1982) assumption of negligible intraspecific geographic variation, but unfortunately neither he nor I yet have data to support our beliefs.

Ni's (1982) third doubtful point concerns the five hypothetical "stocks" delineated by clustering the Division/depth zones. The difficulty of identifying these species, and their overlapping geographic distributions, mean that commercial fishermen will probably always refer to them indiscriminantly as "redfish." Joint quotas will, therefore, have to be set for all *Sebastes* spp. in each area. However, joint assessments of species are fraught with problems (e.g. Paulik et al. 1967; Fukuda 1973; Todd and Smith 1980) and so the assessment units should be monospecific. Furthermore, the term "stock" implies an intraspecific group. If pooled data on two species are examined, they may be expected to indicate specific rather than intraspecific groups. Indeed, this is what Ni's (1982) analysis produced: his five "stocks" encompass respectively (1) a collection of area–depth zones which contain, almost exclusively, *S. mentella*, (2) a second collection that has about two- thirds *S. mentella*, (3) another that has nearly three-quarters *S. mentella*, (4) a heterogenous collection of area–depth zones (from NAFO Division 3L to 4X; a range of some 700 nautical miles) with intermediate mixtures of species, and finally (5) a collection of zones in which *S. fasciatus* predominate. If Ni (1982) had separated the species before analyzing his data, he might have found useful indications of intraspecific groupings. However, the fine scale of genetic

Printed in Canada (J7322a)
Imprimé au Canada (J7322a)

differentiation in these fishes (Altukhov 1974, 1981) and their complex population structures (Kenchington 1982) indicate the need for a different approach. — T. J. KENCHINGTON, *Marine Fish Division, Department of Fisheries and Oceans, Dartmouth, N.S. B2Y 4A2.*

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REPLY

Kenchington (1983) has commented on three aspects of my study of meristic variation in beaked redfishes (Ni 1982). First, he feels I should not publicly propose alternative vernacular names for *Sebastes fasciatus*. "The name for a species may often be decided by weighting the pros and cons among the possible choices and selecting that one which best fits the aggregate of guiding criteria" as described in *A list of Common and Scientific Names of Fishes from the United States and Canada* (American Fisheries Society 1980, p. 5). Proper names for redfishes should, therefore, be discussed publicly by all people concerned before the final decision of the Committee on Names of Fishes of AFS. After the publication of the paper (i.e. Ni 1982), I received comments on the name of *S. fasciatus* from R. N. Lea (Department of Fish and Game, State of California, Monterey, CA) and from D. E. McAllister (Museum of Natural Sciences, National Museums of Canada, Ottawa), who were not aware of the discussion of the names for redfishes. Kenchington indicated that I incorrectly ascribed the name "shelf redfish" to him instead of J. M. McGlade. This "error" was made because the copies of his letter to C. R. Robins (dated April 28, 1982) as well as of W. N. Eschmeyer's letter to Kenchington (May 5, 1982) did not mention that "shelf redfish" was proposed by J. M. McGlade.

Second, Kenchington has criticized my four pieces of evidence in support of the assumptions that the intraspecific variation in anal fin ray and vertebral frequencies of *S. fasciatus* and *S. mentella* is much less than interspecific differences between them. The classification and systematics of sibling redfish species has been confused for decades (Templeman and Sandeman 1957; Barsukov 1968). This has been further confounded by their partially sympatric distribution and possible migration. Barsukov (1972) reported nine distinctive features of the Atlantic species of the genus *Sebastes* and Barsukov and Zakharov (1972) listed 15 morphological characters for differentiating Northwest Atlantic redfishes. They admitted, however, that "all of these external differences are difficult to catch by the eye, especially in the fry; this requires considerable skill" and "it is not very simple to distinguish the rosefish (*S. fasciatus*) from *S. mentella* by its external appearance. Up till now, indeed, it has proved impossible." This is probably why Kenchington insisted that "they did not state how they identified individuals" even if they conducted very thorough morphological observations. From studies of gasbladder musculature (Litvenenko 1980; Ni 1981a), two beaked redfishes (*S. fasciatus* and *S. mentella*) showed significant anatomical differences. From numerical classification studies (Ni 1981b; Misra and Ni 1983), good separations between the two beaked redfish species were demonstrated by discriminant analyses of meristics (100%) and of morphometrics (96%). Morphological guidelines for separation of *S. mentella* and *S. fasciatus* were suggested. Analyses could then be conducted on these good discriminators. However, extensive information collected during Canadian research surveys in the past was of mixed species and therefore of reduced value. My work involved examining the historical meristic data to have "a preliminary understanding of the distribution for *S. mentella* and *S. fasciatus*." The assumption that vertebrae and anal fin ray frequency distributions dominated by 30 and by 8 or 9, respectively, indicated *S. mentella* whereas vertebrae 29 and anal fin rays 7 indicated *S. fasciatus*, was derived mainly from the discriminant analysis of beaked redfishes (Ni 1981b) which had been separated by the anatomical character of extrinsic gasbladder musculature

TABLE 1. The mode of vertebral frequency distribution of beaked redfish by NAFO Division and depth zone. Sample sizes are in Ni (1982, fig. 2).

Depth range (m)	Baffin Bay		Labrador Shelf			NE Nfld.	Flemish Cap	Grand Bank			St. Pierre Bank	Gulf of St. Lawrence			Nova Scotian Shelf		
	0	1	2G	2H	2J	3K	3M	3L	3N	3O	3P	4R	4S	4T	4V	4W	4X
<200		30					29		29	29	29	29	29	29, 30[a]	29	29	29
200–299			30	30	30, 29	30, 29	29, 30	29	29	29	29, 30	30	30	30	29	29	29
300–399	30	30	30	30	30	30, 29	30	29	29	29	30	30	30	30	29	29	29
400–499	30	30	30	30	30	30	30	30, 29	30	29		30	30	30	29	29	29
500–599	30	30	30	30	30	30	30	30	30	30	30, 29				30	29, 30	29
≥600	30	30	30	30	30	30	30	30	30	29, 30					29, 30	30	30

[a]The second figure where shown had a frequency of greater than 35%.

TABLE 2. The mode of the frequency distribution of anal fin rays of beaked redfish by NAFO Division and depth zone. Samples sizes are in Ni (1982, fig. 4).

Depth range (m)	Baffin Bay		Labrador Shelf			NE Nfld.	Flemish Cap	Grand Bank			St. Pierre Bank	Gulf of St. Lawrence			Nova Scotian Shelf		
	0	1	2G	2H	2J	3K	3M	3L	3N	3O	3P	4R	4S	4T	4V	4W	4X
<200		9, 8[a]					7		7	7	7	7	7	8[b]	7	7	7
200–299			9, 8	9	8	8	7	7	7	7	7	8	8	8	7	7	7
300–399	9, 8	9, 8	8, 9	9, 8	9, 8	8, 9	9	7, 8	7	7	8, 7	8	8	8	8	7	7
400–499	8, 9	9, 8	9, 8	9, 8	9, 8	8, 9	9	7, 9	9	7	8	8	8		7, 8	7	7
500–599	9, 8	9, 8	9, 8	9, 8	9, 8		9	9, 8	9, 8	9, 7, 8[c]	9	8				7	7
≥600	9, 8	9, 8	9, 8	9, 8	8, 9	8, 9	9	8, 9	8, 9	7					7	9	9

[a]The second figure where shown had a frequency of greater than 35%.
[b]Samples were mainly collected from 198 to 201 m.
[c]All three figures had a frequency greater than 30%.

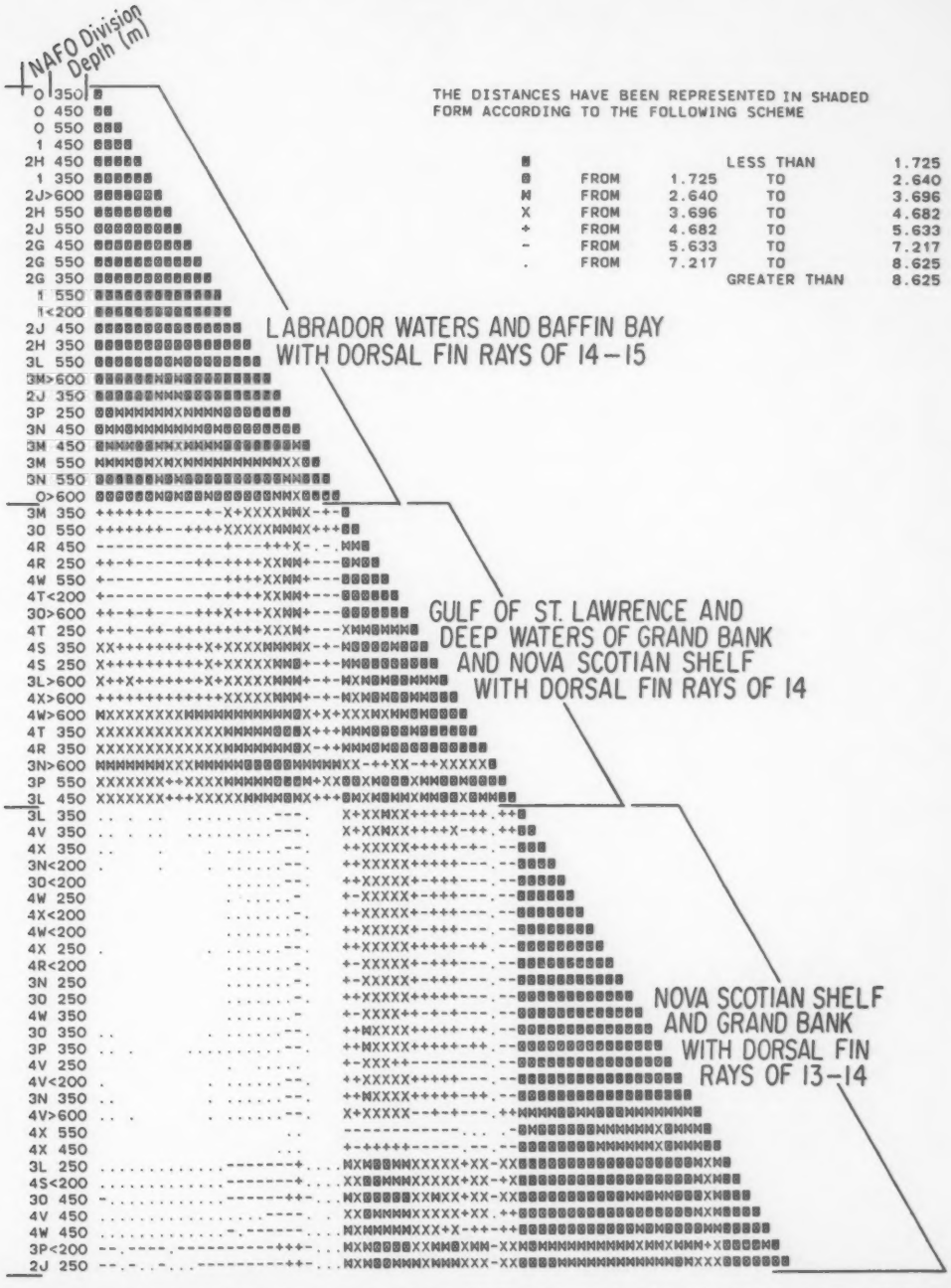
NAFO Division
Depth [m]
THE DISTANCES HAVE BEEN REPRESENTED IN SHADED
FORM ACCORDING TO THE FOLLOWING SCHEME
LESS THAN 1.725
FROM 1.725 TO 2.640
FROM 2.640 TO 3.696
FROM 3.696 TO 4.682
FROM 4.682 TO 5.633
FROM 5.633 TO 7.217
FROM 7.217 TO 8.625
GREATER THAN 8.625
LABRADOR WATERS AND BAFFIN BAY
WITH DORSAL FIN RAYS OF 14–15
GULF OF ST. LAWRENCE AND
DEEP WATERS OF GRAND BANK
AND NOVA SCOTIAN SHELF
WITH DORSAL FIN RAYS OF 14
NOVA SCOTIAN SHELF
AND GRAND BANK
WITH DORSAL FIN
RAYS OF 13–14

FIG. 1. Cluster analysis of dorsal fin ray frequency. Case labels are NAFO division and depth intervals. Depth at 250 represent 200–299 m, same apply to 350, 450, and 550.

(Ni 1981a). I also reminded readers of "the possible geographic variation" (Ni 1981b), but I indicated that "the intraspecific variability is not likely to exceed the interspecific differences" (Ni 1982). I stress that different geographic and vertical patterns of vertebral or anal fin ray frequencies coincide with the results from meristic classification of beaked redfishes (Ni 1981b). This can be clearly exhibited by the different modes of vertebral and anal fin ray frequencies from Division–depth blocks (Tables 1 and 2) since Kenchington (personal communication) said that "My conclusions will be that anal fin ray count can be used to determine the frequency of the species in a sample, but that individual can only be identified by electrophoresis or the gasbladder muscles." Kenchington also argued that meristic characters in these species seem to be correlated, and therefore, "it is hardly surprising that a cluster analysis should group areas with a predominance of low counts separately from areas with predominantly high ones." The cluster analysis on vertebral and anal fin ray frequencies did show two distinct clusters very similar to the one with all three meristic frequencies combined (Ni 1982, fig. 7). However, the cluster analysis on dorsal fin ray frequencies had rather different clusters, particularly for the Gulf of St. Lawrence (Div. 4RST) (Fig. 1). My rationale for these inconsistent characteristics of meristics is that the anal fin ray and vertebrae are good discriminators between the two beaked redfishes whereas the dorsal fin ray is not, as suggested by the discriminant analysis (Ni 1981b).

Finally, Kenchington has criticized the five hypothetical "stocks" delineated by clustering the division/depth zones. Redfish stock assessment and management are ongoing by the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) and Northwest Atlantic Fisheries Organization (NAFO) despite the uncertainties of species/stocks involved. As fisheries biologists, our duties are to improve the stock assessment by the understanding of species/stocks problem and put the most reasonable results into practice as soon as possible. The purpose of the meristic variation study (Ni 1982) was examining the historical data to provide "a preliminary understanding of the distribution for *S. mentella* and *S. fasciatus*" for the future "appropriate design of life history studies of each species and for determining component stocks." The proposed distribution of beaked redfishes (Ni 1982, fig. 8) and stocks (Ni 1982, table 6) is now the new hypothesis to be tested. Furthermore, although "stock" implies an intraspecific group, it ought to be possible to devise for management purposes a "fishery stock" whose members are sufficiently similar in their vital statistics (growth, mortality, etc.) that the data needed for effective management are not obscured.

Indeed, the only character known to be able to distinguish the northwest Atlantic redfishes (*S. mentella*, *S. fasciatus*, and *S. marinus*) is the extrinsic gasbladder musculature (Ni 1981a; Power and Ni 1982). The species distribution, stock unit, and intraspecies geographic variation can only be tested on the same specimens by a combination of studies including examination of gasbladder musculature, biochemical population genetics, and meristics as in a preliminary study by Payne and Ni (1982) — I-H. Ni, *Fisheries Research Branch, Department of Fisheries and Oceans, St. John's, Nfld., A1C 5X1.*

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Printed in Canada (J7322b)
Imprimé au Canada (J7322b)

Simpson's Paradox in Aquatic Data Analysis

Simpson's paradox (Simpson 1951; Blyth 1972) can easily occur in descriptive data analysis. It misleads aquatic researchers, especially those who are not aware of the potential occurrence of this problem in routine data analysis. Two aquatic examples in which Simpson's paradox may occur serve to illustrate this problem.

The first deals with the effects of sea lampreys on lake trout. It is difficult to relate directly changes in abundance of lampreys to changes in either abundance or mortality of lake trout, since data on concurrent populations are often insufficient to establish the relationship. However, wounding rates may be used to indicate the general magnitude of lamprey-induced mortality. The table below shows the wounding rates (B), the wounded individuals in three lengths, C_1, C_2, and C_3, and the total sample size for different length groups of lake trout during the two periods A_1 and A_2 as reported by Wells (1980) and altered, but theoretically possible data in parentheses.

	April (A_1)			Sept.–Oct. (A_2)		
Length group (mm)	Sample size	Wounded fish	Wounding rate (%) (B)	Sample size	Wounded fish	Wounding rate (%) (B)
533–634 (C_1)	184	5	2.7	126	3	2.4
635–735 (C_2)	167	20	12.0	730	29	4.0
					(73)	(10)
736–837 (C_3)	125	14	11.2	498	32	6.4
	(25)	(3)	(12.0)	(698)	(69)	(9.6)
Total	476	39	8.2	1354	64	4.7
	(376)	(28)	(7.4)	(1554)	(145)	(9.3)

If the wounding rate is compared for each length group between the spring and the fall, the wounding rates for the spring are consistently greater than those for the fall in real and altered data; but if the total wounding rate (the total percentage of trout wounded by lamprey) for the spring is compared to that for the fall, one learns that the fall wounding rate is greater than the spring rate. Different conclusions may be drawn as to whether the spring has higher wounding rates or the fall. This inconsistency is a case of Simpson's paradox.

The second example is a hypothetical test of the effectiveness of a new treatment vs. a standard treatment for fish parasites. Since the occurrence of the problem is not limited to a particular species of fish, the fish species in question is not of special concern. The treatment experiments are assumed to be conducted in both the spring and the fall using both the standard and the new treatments.

	New treatment (A_1)			Standard treatment (A_2)		
Time	Sample size	Recovered fish	Percent recovered (B)	Sample size	Recovered fish	Percent recovered (B)
Spring (C_1)	990	99	10	90	5	5.5
Fall (C_2)	120	108	90	980	490	50
Total	1110	207	18.6	1070	495	46.3

The above table shows the hypothetical result that the new treatment has higher recovery rates than the standard treatment for both spring and fall if spring and fall are examined separately; yet if one looks at the total recovery, the standard treatment is more efficient than the new treatment. This inconsistency is also a case of Simpson's paradox.

The reason for the occurrence of this paradox is the large difference in the test populations when used in the form of pair or multiple comparisons or in the form of contingency tables. These large differences can be seen in the examples presented. In the first example, the Sept.–Oct. test populations for the length groups of 635–735 and 735–837 mm (the values in parentheses) were 4.4 and 27.9 times greater than those of the April populations. In the second example, the sample population used in the spring for the new treatment was 11 times greater than that used for the standard treatment at that time, whereas the population used in the fall for the standard treatment was 8.2 fold greater than that examined for the new treatment in the fall.

Such differences are the source of Simpson's paradox, which can be illustrated using a simple probability equation (1) as shown below.

$$(1)\quad P(B/A_1) = P(C_1/A_1) * P(B/A_1C_1) + P(C_2/A_1) * P(B/A_1C_2)$$

$$P(B/A_2) = P(C_1/A_2) * P(B/A_2C_1) + P(C_2/A_2) * P(B/A_2C_2)$$

This formula can be used to illustrate the second example where

$P(B/A_iC_i)$ represents the percentage of recovery within each category,
$P(C_iA_j)$ represents the proportion of sample population used, and
$P(B/A_j)$ represents the total percentage of recovery.

One notes that $P(B/A_1C_1) > P(B/A_2C_1)$ and $P(B/A_1C_2) > P(B/A_2C_2)$ in example 2; but the proportion of fish used in spring (C_1) and fall (C_2) varied greatly, for example $P(C_1/A_1)$ and $P(C_1/A_2)$ are 89 and 8%, respectively, whereas $P(C_2/A_1)$ and $P(C_2/A_2)$ are 11 and 91%. Because of this proportional difference in the sample populations, even if $P(B/A_1C_1) > P(B/A_2C_1)$ and $P(B/A_1C_2) > P(B/A_2C_2)$, $P(B/A_1)$ is smaller than $P(B/A_2)$. The proportion of the sample population is therefore an important factor to consider in categorical comparison. If all proportions of sample population are approximately equal, then the paradox is not likely to occur since $P(C_1/A_1) \doteq P(C_1/A_2)$ and $P(C_2/A_1) \doteq P(C_2/A_2)$. Thus, the primary cause of such misleading conclusions can be attributed to a marked difference in the relative importance of the categories. Avoiding situations in which test populations have large relative differences can reduce the occurrence of this inconsistency.

However, at times situations may arise in which large relative differences in test populations are unavoidable. Under such conditions, Simpson's paradox can occur and one then may face the difficult choice as to whether categorical attributes or summary totals should be used. The appropriate decision in this case depends on whether the change in relative proportion of the test population changes the probability

(percentage) in each category (e.g. length groups and times of the year in the examples). If the answer is no, each category should be weighted equally, then the unweighted average, rather than the summary total, may be used for making inferences. On the other hand, if a change in the relative proportion of sample population in each category greatly affects the probability for that category, then a weighted average or summary total should be used for deriving the experimental conclusion. — WILLIAM Y. B. CHANG, *Great Lakes Research Division, The University of Michigan, Ann Arbor, MI 48109, USA*.

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Printed in Canada (J7162)
Imprimé au Canada (J7162)

BOOK REVIEW/COMPTE RENDU

Ecological Stress and the New York Bight: Science and Management. *Edited by G. F. Mayer. Estuarine Research Federation, Columbia, SC. 1982. 715 p. $10.00 (U.S.), paperback.*

This volume is a compilation of talks and discussions resulting from a 1979 Symposium on the U.S. National Oceanic and Atmospheric Administration's Marine Eco-Systems Analysis conducted on the New York Bight and the estuary of the Hudson River. This Symposium included special attempts to foster communication between scientists, managers, and policy makers. In this regard the book differs from earlier scientific publications emanating from conferences on the Bight. There are five reports of Science Panels written in laymen's terms for nonscientists (Effects of pollutants on benthos, on fishes, and on plankton and neuston; Effects on nutrients and carbon loadings on communities and ecosystems; Effects of toxic substances on communities and ecosystems). The four Management Panels deal with Management of Dredged Material, Industrial Waste, Non-Point Sources, and Domestic Wastes.

It is difficult to determine if all the effort to communicate with policy makers has had any effect, as results would be evident only in the long term. One indication was the judicial decision made in 1981, two years after the Symposium, that New York City could continue to dump sewage sludge into the Bight in spite of an order from the Environmental Protection Agency to move to land disposal. Several of the Science Panels reported that unequivocal relationships could not be established between the impacts of sewage and effects on resources and perhaps the judge took this into consideration. It will be interesting to see if appeal action changes this judgment.

The 33 contributed scientific papers could be placed into the following approximate categories: Benthos/Toxicity, 6; Disease, 4; Resources Species, 3; Benthos/Communities, 5; Microbiological, 3; Plankton/Nutrients, 9; and General/Comparative, 3. The general papers contrast the Bight with benthic ecosystems in California and Florida, and bring some theoretical thoughts to bear on a difficult applied problem. Thirty-nine percent of the papers deal with benthic species or benthic communities as accumulators of contaminants or integrators of degraded benthic conditions, and are an excellent source of ideas and references to these and other benthic topics. In spite of these efforts it was not possible to predict effects of benthic disruption on commercially important fish and shellfish, but the effects are certainly present. There have been important shifts in the Bight in types of benthic animals available for fish, for example, from amphipods which are used to certain polychaetes which are not, but effects on fish production cannot be deduced. The paper on oysters by Franz provides good information on the direct and dramatic impact of pollution on a commercially significant benthic organism. Other benthic species' marketability has been reduced by pollution-related diseases such as shell disease, fin rot, and black gill disease. Commercial fishing has been banned in the lower Hudson River since 1975 because of PCB contamination. Polynuclear aromatic hydrocarbons are present in many benthic species in the inner New York Bight and the lower Hudson–Raritan estuary. Sewage sludge affects sediment conditions further offshore.

The various components of the New York Bight research have been conducted separately, and the book does represent a compilation of talks rather than synthesis of planned research. The overall study strategy demonstrated in the volume should not be adopted by others who might be attempting a reductionist approach to marine pollution, as the Symposium focused on end effects. If the object is to face the problem head on with pragmatic pollution control officers, this volume does provide some guidelines on how to gather the most useful data. The concept of arranging scientific and management panels to explain strengths and weaknesses of the results is a good idea, and the Estuarine Research Federation should be commended for attempts to bring scientists and policy makers together. This job is often thankless scientifically.

In spite of its rather mixed content, the book is especially recommended to research managers concerned with conveying results to user groups, such as treatment plant administrators, and to applied benthic ecologists. Details are provided on the waste disposal problems of one of the largest cities in the world, and the volume is interesting from this aspect alone.

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ANNOUNCEMENTS/AVIS

Society of Canadian Limnologists

The Society of Canadian Limnologists (SCL) affiliated with Societas Internationalis Limnological (SIL), meets annually in January in conjunction with the Canadian Conference for Fisheries Research (C.C.F.F.R.) and the Canadian Society of Environmental Biologists (CSEB).

The aim of S.C.L. is the advancement of all branches of theoretical and applied limnology (physical, chemical, and biological) in Canada. The Society promotes not only the scientific aspects of limnology but also better public understanding of the fundamental importance of inland waters to Canada.

The annual and other meetings permit limnologists in Canada to exchange scientific information and views on environmental issues of regional and national concern. S.C.L. also serves as a forum to focus the concerns of members so that Canadian positions can be presented at international meetings including S.I.L.

There are three categories of members:

a) International members, i.e. members of both S.I.L. and S.C.L. membership fee for 1983 — $10.00 plus the current S.I.L. fee of $25.50 Can. (Total $35.50 Can.) International members who maintain membership receive all S.I.L. publications.
b) General members, i.e. members of S.C.L. only, membership fee for 1983 — $15.00.
c) Student members, i.e. members enrolled in undergraduate or graduate programs in Canadian universities, membership fee $5.00.

Members receive newsletters, meeting programs and abstracts. For additional information please contact: *F. J. Ward, Secretary-Treasurer, Department of Zoology, University of Manitoba, Winnipeg, Manitoba, R3T 2N2. Telephone: (204) 474-9683.*

Société canadienne des limnologistes

La Société canadienne des limnologistes (SCL), affiliée à la Societas Internationalis Limnological (SIL), se réunit chaque année au mois de janvier en même temps que la Conférence canadienne relative à la recherche sur les pêches (CCRRP) et la Société canadienne des biologistes de la faune (SCBF).

La SCL vise l'avancement de tous les domaines de la limnologie théorique et appliquée (physique, chimique et biologique) au Canada. Elle encourage non seulement les aspects scientifiques de la limnologie, mais cherche à sensibiliser le grand public quant à l'importance fondamentale des eaux intérieures pour le Canada.

Les réunions annuelles et autres permettent aux limnologistes canadiens d'échanger opinions et information scientifique sur les questions environnementales d'intérêt régional ou national. La SCL sert aussi de tribune libre où les membres peuvent soulever leurs préoccupations et où la position du Canada peut être précisée en vue de sa présentation aux réunions internationales, dont celle de la SIL.

Il existe trois catégories de membres soit :

a) les membres internationaux qui font partie de la SIL et de la SCL; la cotisation pour 1983 s'élève à 10,00 $, outre la cotisation à la SIL, qui est de 25,50 $, pour un total de 35,50 $ CAN. Le membre international qui a payé sa cotisation reçoit toutes les publications de la SIL.
b) les membres généraux qui font partie de la SCL dont la cotisation est fixée à 15,00 $ pour 1983;
c) les membres étudiants qui sont enregistrés à un programme de premier ou de deuxième cycle dans une université canadienne; la cotisation s'élève à 5,00 $.

Les membres reçoivent le bulletin d'information, les programmes et les résumés des réunions. Pour de plus amples informations, prière de contacter : *F. J. Ward, secrétaire trésorier, Département de Zoologie, Université du Manitoba, Winnipeg (Manitoba) R3T 2N2. Téléphone : (204) 474-9683.*

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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

CJFSDX40(9) 1331–1542 (1983)
ISSN 0706-652X

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